B.

MALE.

FEMALE.

MALE AND FEMALE WOOD DUCK, TO SHOW SECONDARY SEXUAL CHARACTERS.

[From photographs of stuffed specimens in the Collection of the Maryland Academy of Sciences.]

THE LAW OF HEREDITY.

A STUDY OF THE

CAUSE OF VARIATION,

AND THE

ORIGIN OF LIVING ORGANISMS.

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TO

THE MEMORY OF

CHARLES DARWIN,

FROM WHOSE STORE OF PUBLISHED FACTS I HAVE DRAWN MOST OF THE MATERIAL FOR THIS VOLUME.

PREFACE.

The subject which is treated in this book has occupied my thoughts for ten years or more, but I have refrained from publishing my views, as I hope that I may some time be able to submit them to the test of experiment.

Many experiments have suggested themselves to me, but as most of them involve the cultivation and hybridization, for many generations, of such animals and plants as will thrive and multiply in confinement, they can only be carried out by some one who has the means for experimental researches, and who has also a permanent home in the country, where organisms of many kinds may be kept under observation for years, and where many specimens of hybrids between various wild and domesticated species can be reared to maturity.

My own studies have been in a different province of natural science, and it has therefore seemed best to publish this volume in order to call renewed attention to this most fascinating subject.

I have little hope that my views will be permanently accepted in the form in which they are here presented, but I do hope that they may serve to bind together and

to vitalize the mass of facts which we already possess, and that they may thus incite and direct new experiments.

If this book should serve to turn the attention of others into this channel, and should thus ultimately help us to a clearer insight into the nature of the forces which have acted, and still act, to guide the evolution of life, this result will far outweigh the acceptance or rejection of the speculations which are here advanced.

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HEREDITY.

CHAPTER I.

WHAT IS HEREDITY?

The development of an animal, with the complex and beautiful structural adjustments, the instincts, habits, and individual traits of its parents is one of the most wonderful phenomena of the material universe—Heredity is not due to the external conditions which act upon the ovum, but to something within the ovum itself—The phenomena of reversion—Asexual and sexual heredity—Possibility of an explanation of heredity—Characteristics which are now hereditary were at one time new variations—Heredity and variation are opposite aspects of the same problem—We may hope that a more perfect acquaintance with the laws of heredity will remove many objections to the theory of natural selection.

To the ordinary unscientific reader the word heredity may perhaps suggest nothing more than a few curious cases where an odd peculiarity of the parent has been transmitted to the children, or it may recall the hereditary transmission of a tendency to certain diseases, or the mental or moral idiosyncrasies of the parents.

To the breeder of domestic animals or plants it has a somewhat wider significance, and recalls the transmission by choice or fancy breeds of the features which give them their value. To him heredity is the law which enables him to modify his animals and to build up and perpetuate new varieties.

To the naturalist, on the contrary, the word is filled with deep meaning, and instead of recalling to his mind a few odd cases, the tricks and accidents of heredity, it brings before him the most marvellous of all the phenomena of the material universe: the production from a simple egg of a living animal, with the intricate structure and complex bodily and mental functions of its proper species.

Thoughtful men of all ages have regarded the structure and faculties of the higher animals as a proper field for life-long study. Yet the acute intellects, the powers of patient observation and profound reflection which generations of naturalists have brought to this fascinating subject, have not yet given us a complete knowledge of the life of a single animal.

In every age and country where science has flourished men have devoted their lives to this subject, and have felt that their hardly-earned results could scarcely be called a beginning. So vast is the field, so many are the phenomena, that the province of natural science is practically infinite, for each animal and each plant presents special problems which open out in all directions before the student in an endless vista.

Wonderful and various as the attributes of each animal are, however, they are not mysterious; for, at the same time that we discover in an organism the power to do wonderful things, we also find in it a material organization, a mechanism, adopted to do these very things. It is true that we cannot perfectly understand this mechanism, that in many cases we fail completely in our attempts to trace its working, and that in most cases our insight is very crude indeed. Still we are able to show that the machinery exists; and anatomy, or the study of structure, goes hand in hand with the study of the bodily

and mental activities of animals. We do not understand the machinery, but we find that it is there, and we can interrupt its work by obstructing or injuring it. Our wonder is not a feeling of mystery, a sense that the phenomena transcend knowledge; it is due to a perception of the amount of knowledge required. We regard an adult animal with feelings similar to those with which an intelligent savage might regard a telephone or a steamboat.

A dog, with all the powers and faculties which enable him to fill his place as man's companion, is a wonder almost beyond our powers of expression; but we find in his body the machinery of muscles and veins, digestive, respiratory, and circulatory organs, eyes, ears, etc., which adapts him to his place; and study has taught us enough about the action of this machinery to assure us that greater knowledge would show us, in the structure of the dog, an explanation of all that fits the dog for his life; an explanation as satisfactory as that which a savage might reach, in the case of the steamboat, by studying its anatomy.

Let our savage find, however, while studying an iron steamboat that small masses of iron, without structure, so far as the means at his command allow him to examine and decide, are from time to time broken off and thrown overboard, and that each of these contains in itself the power to build up all the machinery and appliances of a perfect steamboat. The wonderful thing now is not the adaptation of wonderful machinery to produce wonderful results, but the production of wonderful results without any discoverable mechanism; and this is, in outline, the problem which is brought before the mind of the naturalist by the word heredity.

Every one knows that each dog exists at some time

as an egg, and the microscope shows in this egg no traces of the organs of the dog's body or of anything at all like them. So far as our means of examination go the egg is no more like a dog than the mass of iron is like a steamboat. It may be said, though, that the dog's egg is not left to itself, but is fertilized and is carried inside the body of the mother until the new animal is matured; that it is there nourished and built up from substances supplied through the body of a full-grown dog; that it may be acted upon at this time by agencies which have a direct tendency to build up out of it an organism like the parent; that the egg does not actually contain a potential dog, but simply supplies the proper material to be acted upon by the surrounding conditions, and that the structure of the new animal is due to these conditions; that the embryo becomes a dog because it is bathed by a dog's blood, nourished through a dog's body, and is completely surrounded by influences which are peculiar to dog nature. Those persons who are not naturalists derive their knowledge of the animal world chiefly from our common domestic animals, and to such persons this explanation may seem probable; but naturalists, with wider experience, know that animals which carry their young inside their bodies are exceptions, and that the organization of the future animal must exist potentially in the egg, since the conditions to which it is exposed cannot possibly have any tendency to produce from it a being which does not already exist, in some form, within it.

A bee is almost as wonderful as a dog; its anatomical structure is exquisitely delicate and complex, and every one is acquainted with the wonderful work which it accomplishes. At the time it is laid the egg which is to become a worker-bee contains no visible trace of its

body, or of anything like it. It has been carefully studied with all the resources of modern science, but examination shows nothing within it which is more like a bee than a mass of iron is like an iron ship. This egg is not even fertilized, but it develops into a perfect worker, with all its wonderful structure and instincts, by virtue of something which it contained when it left the ovary of its mother. It is true that it is not left quite to itself, but is carefully attended and cared for by other bees; but everything which they do for it might be done just as well by delicate machinery, and the attention has no tendency whatever to manufacture a bee. Proper heat and access to air are as necessary as attention, and attention has no more power to produce a bee than air or heat.

No one who is familiar with marine animals can believe for an instant that the conditions to which an egg is exposed have anything whatever to do with the character of the animal to which it gives rise. We may artificially remove eggs from the ovaries of several different animals, fertilize them artificially, and then place them together in a tumbler of sea water, and expose them to exactly similar external conditions, yet each one will follow its own determined course, and we may rear in the same tumbler of water from eggs which are hardly distinguishable animals which have less in common than a dog and a bird.

If there is no mystery in the performance by the complicated organs of an adult animal of all its complicated functions, what shall we say when we find the power to perform these functions existing in a latent state in the egg, without the corresponding organs?

This is the problem of heredity. In the mind of the naturalist the word calls up the greatest of all the wonders of the material universe: the existence, in a simple,

unorganized egg, of a power to produce a definite adult animal, with all its characteristics, even down to the slightest accidental peculiarity of its parents; a power to reproduce in it all their habits and instincts, and even the slightest trick of speech or action.

This is by no means the whole of the problem of heredity. One of the most interesting phenomena connected with our subject is what is known as reversion, or the appearance in the child of peculiarities which were not present in either parent, but are due to inheritance from a grandparent or a more remote ancestor. An interesting illustration of this law is the occasional appearance in horses of stripes on the body and legs. Such stripes are not usually present in the horse, although Darwin has given reasons for believing that our horses are descended from a striped zebra-like ancestor. The power to revert to this ancestral form is handed down from generation to generation in the egg, and it may show itself at any time by the production of a striped colt. Reversion is, in a certain sense, exceptional, but it is not at all rare, and we must add this power to the wonderful properties of the egg.

Darwin gives the following case, which will serve to illustrate the nature of reversion: A pointer bitch produced some puppies; four were marked with blue and white, which is so unusual a color in pointers that she was thought to have played false with one of the greyhounds, and the whole litter was condemned, but the gamekeeper was permitted to save one as a curiosity. Two years afterwards a friend of the owner saw the young dog, and declared that he was the image of his old pointer bitch, Sappho, the only blue and white pointer of pure descent which he had ever seen. This led to close inquiry, and it was proved that he was the great-

great-grandson of Sappho; so that, according to the common expression, he had only one-sixteenth of her blood in his veins.

Another aspect of our subject must be kept constantly in mind. Among the higher animals heredity usually manifests itself only by what is known as sexual reproduction,—that is, the development of new individuals from fertilized eggs; but in the lower forms of life another kind of reproduction, the development of new individuals by budding or by analogous processes, is even more common. Among the hydroids heredity may manifest itself by the formation of new animals, with all the characteristics of the parent, on almost any part of the body of the latter, and in certain plants the smallest fragment of tissue may become a new and perfect plant, capable of producing others in the same way or by seeds. The most sure and rapid way to get new sea-anemones is to tear an old one to pieces. As a rule this power is confined to the lower forms of life, but certain animals which are by no means low or simple in structure multiply asexually, and the offspring thus produced inherit, like those developed from eggs, all the characteristics of the parent.

This then is the problem of heredity, certainly one of the grandest secrets of nature. When we reflect upon its obscurity and complexity we may fairly ask what hope there is of discovering its solution; of reaching its true meaning, its hidden laws and causes. If it is true that, in each egg, all the functions and faculties of a definite mature animal lie hidden, without any corresponding organs, must we not regard heredity as a mystery too great for solution; as something which must be accepted as it is without scientific explanation?

Thirty years ago the adaptation of each organ of an

adult animal to its proper purpose seemed to be a mystery of the same kind, and many profound thinkers satisfied themselves and taught others that this adaptation was not brought about by the laws of matter and by secondary causes; that it must be accepted in itself, without explanation, and that the methods of physical science are here of no use.

Darwin's work has taught us that this is not true; that in the law of natural selection we have at least a partial explanation of the origin of the adaptation of nature; that while natural selection may not be the exclusive means by which they have been produced, it is, so far as it goes, a true scientific explanation, for it even puts it in our power to produce, in domestic animals, similar adaptations to special purposes, by the selection of the fittest variations.

Darwin, in his first and in all his later books on the subject, pointed out that his discovery did not complete the solution of the problem; that "natural selection is a great but not the exclusive means of modification." The greatest value of his work lies in the proof which he has furnished, that the origin of the structure of animals is not beyond our reach, but that observation and reflection, the means which have unlocked for us so many of the secrets of inorganic nature, are equally useful in this field; that the adaptations of nature may be studied and understood like a problem in astronomy or physics.

The aim of this work is to show that the same thing is true of the problem of heredity.

We may not be able, as yet, to penetrate its secrets to their inmost depths, but I hope to show that observation and reflection do enable us to discover some of the laws upon which heredity depends, and do furnish us with at

least a partial solution of the problem; that we have every reason to hope that in time its hidden causes will all be made clear, and that its only mystery is that which it shares with all the phenomena of the universe.

In this introductory statement we have presented one side of the problem of heredity: the transmission from parent to child of the established congenital hereditary characteristics of the race. We must not forget, though, that there is another aspect which is fully equal to this in importance. We know that each characteristic has been gradually acquired through a long series of modifications; that all the wonderful adaptations which fit animals to their surroundings, and meet their particular needs, has been evolved step by step by the natural selection of the fittest congenital variations. Each race-characteristic has at one time been a new variation, and the process of modification is still going on and perfecting the harmony between the structure of each organism and its needs. No theory of heredity has any value unless it explains the way in which new features, which may become hereditary, continually make their appearance as congenital variations, at the same time that it accounts for the way in which established peculiarities are handed down from generation to generation.

The problem is two-sided; what is now hereditary was at one time variation, and each new variation may soon be hereditary. Heredity and variation are opposite aspects of the same thing, and an explanation must be examined and tested on the one side, as well as on the other, before it can be accepted.

There is still another consideration which remains to be noticed.

Darwin has never failed to perceive, and he has frequently pointed out, that the law of natural selection is not

a complete explanation of the origin of species, and that it is exposed to certain very serious difficulties.

Still he concludes that the theory is supported by such a mass of evidence that we may fairly believe that our own knowledge, not natural selection, is at fault, and that further research will remove the difficulties by the discovery of other laws.

Naturalists all over the world have acknowledged the justice of this claim, and some, less candid and broad-minded than Darwin, seem to have even lost sight of the difficulties.

Now natural selection can act only by the preservation of such variations as chance to appear, and until we know the laws which govern the appearance of variations it must be impossible to decide how far the course of organic evolution has been determined by these unknown laws, and how far by natural selection.

We may therefore entertain a reasonable hope, that when the true theory of heredity is discovered, it will, by revealing to us the laws and causes of variation, place the law of natural selection upon a firmer basis, and show that its apparent difficulties are simply due to the narrow limits of our knowledge.

With this introduction I will pass to the discussion of our subject, the nature of heredity.

The attempt to generalize from the whole field of natural science is beset with many difficulties, since the field is so vast that an attempt to give in advance a statement of all the facts upon which reasoning is based would simply confuse the mind of the reader, and burden him with a mass of detail.

It seems best then to start with the generalizations which are believed to bind the facts together, so that the reader may then approach the specific proofs with more

interest. The latter method is open to objection, since the reader may be called upon to listen to views which are opposed by accepted authorities, and to wait until the proofs are presented in due course.

I must therefore request the reader to suspend judgment, and to lay aside established opinions, until he has examined the subject upon all sides.

The examination of the history of the subject will furnish an introduction to its scientific discussion, and I have therefore adopted the following plan:

I shall give, first, an outline of the chief hypotheses which have been proposed, from time to time, as an explanation of heredity, with reasons for rejecting them. I shall then present briefly, in outline, a statement of what I believe to be the true explanation. I shall then try to show that this theory furnishes a basis or foundation for the theory of natural selection, and removes the most serious difficulties which have been urged against the latter theory. I shall then show that there is no *a priori* reason for rejecting the theory of heredity; and that it furnishes an explanation of many well-known facts which cannot without it be seen in their true relations. I shall then attempt to show that it is supported by direct proof, and finally I shall give a statement of the theory in a more extended form.

CHAPTER II.

HISTORY OF THE THEORY OF HEREDITY.

Requisites of a theory of heredity.—Historical sketch of speculation on heredity—Evolution hypothesis of Bonnet and Haller—Ovists and spermists—Modern embryological research has shown that it is impossible to accept the evolution hypothesis in its original form—Buffon's speculations upon heredity fails to account for variation—Hypothesis of epigenesis—This hypothesis is logically incomplete—The analogy between phylogeny and ontogeny gives no real explanation of the properties of the ovum—Haeckel's plastidule hypothesis —This hypothesis is not logically complete unless it involves the idea of evolution—Jager's hypothesis—Ultimate analysis shows that this is at bottom an evolution hypothesis—No hypothesis of epigenesis is satisfactory—No escape from some form of the evolution hypothesis—This conclusion is accepted by Huxley.

§ 1. *Requisites of a theory of heredity.*

The following list is a brief summary of what seem to me the most important characteristics of the reproductive process in living things:

1. New organisms may be produced by the various forms of asexual generation and from ova.

2. Ova may develop, in certain cases, without fertilization.

3. As a rule the ovum does not develop into a new organism until it has been fertilized by union with a male cell.

4. The ovum and male cell will not unite unless they are derived from organisms with the same or nearly the same systematic affinities.

5. The new organism, whether produced sexually or asexually, is essentially like its ancestors, although it may be quite different from its immediate ancestor, as in cases of alternation.

6. Organisms produced from fertilized ova differ in the following points from those produced asexually:

a. As a rule the development of the egg embryo is indirect, and a more or less complicated metamorphosis or alternation of generations must be passed through before the adult form is reached, and the circuitous path thus traversed bears a resemblance to the line of evolution of the species. An organism formed asexually traverses only so much of this path as remains to be traversed by the organism which gives birth to it.

b. Reversion, or the appearance of characteristics not exhibited by the parents, but inherited from remote ancestors, is not at all unusual in egg embryos, but it is more rare in those produced asexually.

c. New variations, or features which are not inherited, appear continually in organisms produced from fertilized ova, and they may be transmitted either sexually or asexually to future generations, thus becoming established as hereditary race-characteristics. Hereditary variations are extremely rare in organisms produced asexually.

7. The ovum and the male cell are homologous with each other, and are morphologically equivalent to the other cells of the organism. We must therefore believe that their distinctive properties have been gradually acquired, and that their specialization has been brought about by the action of the same laws as those in accordance with which the other specializations of the organism have been produced.

8. Changed conditions do not act directly, but they cause subsequent generations to vary.

9. In the higher animals, where the sexes have long been separated the male is more variable than the female.

10. The result of crossing is not the same when crosses are made reciprocally.

11. The sex of the parent-species affects the degree of variability of hybrids; and when a hybrid is used as the father, and either one of the pure parent-species, or a third species, as the mother, the offspring are more variable than when the same hybrid is used as the mother and either pure parent-species or the same third species as the father.

There may perhaps be other requisites which should be included in this list, but I think there can be no doubt that a theory of heredity must recognize and be in harmony with all which are here given.

§ 2. *A sketch of the history of speculation on the theory of heredity.*

The laborious researches of the students of the science of embryology have yielded a rich harvest of valuable facts, and we now know that the process of cell division by which an unspecialized unicellular egg becomes converted into a many-celled, highly-specialized organism bears the closest resemblance to the process of growth or of ordinary cell-multiplication.

We know that all the various forms of reproduction, cell-multiplication, fission, gemmation, conjugation, sexual reproduction, and parthenogenesis, are inter-related in such a way that we must believe that they are different manifestations of the same power, and that they have been evolved one from the other.

We know that direct development, metamorphosis, and alternation of generations are not separated from each other by any hard and fast line, and we know too that

the changes through which the embryo passes on its road from the egg to maturity show a wonderful parallelism to the series of changes through which the organism has passed during the history of its evolution from lower forms.

These results are well worth the labor they have cost, and they illustrate, more clearly than any other facts in biology, the common nature of all living things. They do not, however, contribute directly to a clearer insight into the laws of heredity.

Here we are still compelled to go beyond the visible phenomena, and to attempt by the scientific use of the imagination to discover the as yet unseen relations which bind them together.

As we enter upon this subject it will be well to bear in mind the wide difference between the end we have in view—the discovery of the secondary laws of heredity—and the attempt to understand its ultimate cause.

The power to reproduce itself, to impress upon dead inorganic matter its own distinctive properties, is one of the fundamental characteristics of living matter; and while we may hope that increase of knowledge may some day enable us to trace the origin of this power, such an attempt forms no part of our present undertaking.

We shall accept without explanation the fact that living matter does thus reproduce itself, and we shall confine ourselves to the attempt to discover why the egg of a star-fish for instance, reproduces a star-fish, and the egg of a bee a bee; to discover the origin of the differences between the various forms of reproduction, rather than the cause of what they have in common.

The phenomena of heredity in the higher animals, as well as the mechanism of ova and male cells through which these phenomena are manifested, have certainly

been produced by slow modification, through the influence of conditions which are to a great extent open to study. The attempt to trace their origin and significance is not a pure speculation, but a legitimate exercise for the scientific intellect.

As we should expect from the fascinating nature of the subject, there has been no lack of speculation in the past, and various hypotheses have been proposed from time to time to account for the phenomena of heredity. These hypotheses differ greatly among themselves, but they may beroughly classed as epigenesis hypotheses, and evolution hypothesis: the word evolution being here used, of course, in its old sense, as contrasted with epigenesis.

The hypothesis of evolution, pure and simple, as advocated by Bonnet and Haller, is that there is contained in the egg or seed or in the male element a perfect but minute organism, and that the subsequent development of the egg is simply the "evolution" or unfolding of this germ. Up to the end of the last century the prevailing opinion was that each egg contains, in a latent or dormant state, a completely formed organism. The fertilization of the egg was supposed to awaken this dormant germ, to call its latent potential life into activity; and the process of development was regarded as the unfolding and growth of the already fully formed and perfect embryo. The embryo was held to be not produced by, but simply unfolded from the egg, and the act of reproduction was therefore regarded as *eduction* not *production*.

According to Huxley (Encyc. Brit., Art. Evolution) "Bonnet affirms that before fecundation the hen's egg contains an excessively minute but complete chick, and that fecundation and incubation simply cause this germ to absorb nutritious matters, which are deposited in the interstices of the elementary structure of which the min-

iature chick or germ is made up. The consequence of this intussusceptive growth is the "development" or "evolution" of this germ into the visible bird. Thus an organized individual "is a composite body consisting of the original or elementary parts, and of the matters which have been associated with them by the aid of nutrition," so that if these matters could be extracted from the individual, it would, so to speak, become concentrated in a point, and would thus be restored to its primitive condition of a germ "just as by extracting from a bone the calcareous substance which is the source of its hardness it is reduced to its primitive state of gristle and membrane."

"*Evolution* and *development* are, for Bonnet, synonymous terms; and since, by *evolution* he means simply the expansion of that which was invisible into visibility, he was naturally led to the conclusion, at which Leibnitz had arrived by a different line of reasoning, that no such thing as generation exists in nature. The growth of an organism being simply a process of enlargement, as a particle of dry gelatine may swell up by the intussusception of water, its death is a shrinkage, such as the melted jelly might undergo on desiccation."

Much more anciently the evolution hypothesis found acceptance in a somewhat different form, and the miniature organism was believed to exist in the male element, and to receive from the egg the nourishment needed for its growth and perfect development.

Loeuwenhoeck's discovery of the motile spermatozoa of animals was regarded as a new basis for this view, and the "sperm-animalcule" was held to be the perfect and living animal ready for unfolding or evolution, the term "spermatozoon," still retained in scientific nomenclature, being a remnant of this old hypothesis. Loeuwenhoeck's

discovery inaugurated, in the first half of the last century, the warm dispute between the Animalculists and the Ovists, one side holding that the germ is contained in the egg, and the other that it exists as the seminal animalcule.

It is obvious that, in either form, the evolution theory, as above stated, is logically incomplete, since it only accounts for a single generation. Its advocates were therefore compelled to enlarge it, and to assume that, as each organism thus exists, in a perfect form, in the preceding generation, each germ must contain, on a still smaller scale, the perfect germs of all subsequent generations. Thus Bonnet held, in his hypothesis of emboitement, "that all living things proceed from pre-existing germs, and that these contain, one inclosed within the other, the germs of all future living things; that nothing really new is produced in the living world, but that the germs which develop have existed since the beginning of things." (Huxley, Evolution.)

The advocates of the evolution hypothesis appealed to such facts as the presence of a minute plant inside the acorn, or to the butterfly inside the pupa-skin, in support of their views; but the hypothesis, in its crude state, was quickly overthrown by the first discoveries of modern microscopic embryology.

Harvey's studies on the development of the chick, followed by the researches of Wolff, Pander, Von Baer, and the host of embryologists of the last fifty years, show conclusively that the embryo is not unfolded out of, but gradually built up from the egg.

We now know that the eggs of all animals, when they are not complicated by the presence of food, or of peculiar coverings for protection or attachment, are essentially alike in optical structure, and that they are not only like

each other, but like the constituent cells of all parts of the body of the organism.

Far from being ~~performed~~ preformed in the egg, we know that the body is built up gradually, step by step, by repeated cell-division, and that the earlier stages of development do not result in the formation of the parts of the perfect body at all, but that they simply give rise to germ-layers, or tracts of cells out of which organs are gradually formed, and that cells which were at first quite widely separated in the embryo may come at last to enter into the formation of a single organ.

For instance, when the nervous system of a vertebrate first makes its appearance in the embryo, there are no traces of the brain, of the spinal cord, of the nerves or of sense organs. It at first consists of a long group of cells running along the middle line of the body, and presenting no difference from the other cells of its surface. In most cases this elongated group of cells becomes converted into a furrow, and afterwards into a closed tube, the nerve-tube, by the folding together of its edges. The primitive nerve-tube is at first simply a long tube of embryonic cells running along the middle line of the back, and it is a very different thing from the final nervous system of an adult mammal, nor is it in any sense a mammalian nervous system in miniature, for the changes by which it becomes converted into the latter are great and numerous, as well as gradual. Certain parts, such as the eye, are formed only in part from this tract of cells, for the vertebrate eye is the result of the combination of an outgrowth from the embryonic nervous system and an ingrowth from the surface of the head.

The whole history of the nervous system and sense organs is thus seen to directly oppose the view that these organs are present in miniature in the germ.

Still more opposed to the hypothesis of evolution is the remarkable fact that the changes which take place in the developing egg are not such as would lead directly to the formation of the adult animal. In most cases a circuitous or indirect path is followed, and this indirect path leads at first towards the adult form of lower members of the group.

This, the most suggestive fact of modern embryology, may perhaps be made clearer by an illustration.

Let us try to compare the growth of an egg into an adult animal with the growth of some manufactured product in the hands of its maker.

The evolutionist view of the development of an organism may be illustrated by the manufacture of a yarn base-ball. A boy, wishing to make a yarn ball, procures, if possible, a small rubber ball, and winds his yarn onto this until the desired size is reached, the only changes during the growth of the ball being the change of size and of material.

The observed facts of embryology show that the development of an embryo does not take place in any such way as this. It may, however, be illustrated by the growth of a steam-ship in the hands of the builder, who first lays down an indefinite skeleton, and outlines in a vague way the more prominent features, before any of the details are finished. In order to make the illustration perfect, however, we must imagine the builder to commence work upon his steam-ship by laying out the skeleton of a big triareme; we must imagine him to carry this some stages towards completion, and to put into it certain contrivances, such as rowers' benches, which are of no use in a steam-ship. We must imagine that he then abandons his plan, tears down his benches, and uses the material to make a deck; that he changes the shape and

proportions of his hull a little to fit it for sailing instead of rowing, that he puts in masts and spars, and makes everything ready for a ship's rigging; that he then changes the shape of his hull once more; tears out part of his cabin, puts in bulkheads, coal bunkers, and an engine and boiler; shortens his masts, alters his rigging, and finally converts his unfinished ship into a finished steamer.

This is not by any means a forced illustration, but a very fair outline of the development of an animal. In nearly every case we find that the development of the embryo as a whole, or else the development of certain organs, takes place in this roundabout, indirect way, and repeats, usually in an imperfect manner, the structure of a related but lower animal.

As an example, we may refer to the history of the blood-vessels of a mammal. The breathing organs of the lower vertebrates are gills on the sides of the neck, and the venous blood is driven from the heart through a series of branchial arteries to the gills, where it is aerated and conveyed into a series of branchial veins which carry it, not back to the heart, but to the various organs of the body. In a mammal there are no traces of gills at any stage of development; the adult animal breathes by lungs, and the blood which has been aerated in the lungs goes back to the heart before it is distributed throughout the body. Now the early stages in the development of the blood-vessels of a mammal would, if carried out to completion, lead to the formation of the system found in fishes.

The mammalian embryo has no gills, but it does have branchial arteries and veins, and its blood at first follows the same course that it follows in a fish. It is plain that the fish-like circulation is not an outline or sketch of that of a mammal; that it is not a necessary stage in

the formation of the latter, for the branchial vessels are soon, in part pulled down and destroyed, and in part profoundly modified, in order to conform to the mammalian type.

Cases of this kind are almost universal, and the law of resemblance between the early stages of higher animals and the adult condition of lower animals is a fundamental law of embryology.

It is obvious that the hypothesis of evolution of a perfectly formed germ contained in the egg, is utterly irreconcilable with this law, and we may therefore state with confidence that this hypothesis is refuted by the observed facts of embryology.

We must not forget, however, that there were other less superficial forms of the evolution hypothesis, and that these cannot be disproved so easily.

Buffon, for instance, held that the embryo is built up by the union of organic particles which are given off from every part of the body of the parent, and which, assembling in the sexual secretions, assume in the body of the offspring positions like those which they occupied in the parent. This is essentially an evolution hypothesis, but it is logically complete, since it accounts for the production of successive generations without the necessity for assuming that they were all contained in embryo in the body of a remote ancestor. Microscopic examination cannot overthrow this hypothesis, for a failure to discover these organic particles with any particular magnifying power does not, of course, disprove their existence any more than a failure to see them without a microscope.

Although Buffon's hypothesis does not account for the fact that development is indirect in most cases, that the egg does not build up the adult animal in the simplest way, but takes a roundabout circuit, this fact is not

directly opposed to his hypothesis, for we can easily conceive that after an indirect method of development has been established it might be perpetuated by Buffon's organic molecules, provided these are given off by the parent organism at all stages of its life, and not simply after it has reached its final form.

There is, however, another class of phenomena of even greater importance—the phenomena of variation.

Buffon's hypothesis accounts for the resemblance between the child and the parents, but we now know that the child is not exactly like its parents or even midway between them, that animals and plants are born with a tendency to vary, that this variation may affect any part of the body, and that by the selection of these congenital variations the most profound changes of hereditary structure may be produced.

The fact of congenital variation is as profound, as universal, and as characteristic of living things as the fact of heredity, and the constant appearance of new variations is as fatal to Buffon's hypothesis of evolution as it is to that of Bonnet.

With the growth of the modern science of morphology these hypotheses have been abandoned and the hypothesis of epigenesis almost universally accepted in their place.

This hypothesis, first brought into notice by the researches of Harvey and Wolff on the development of the chick, has gradually assumed a more definite shape with the progress of embryology, and has been especially modified by the growth of the cell theory.

In its modern form it may, for convenience of discussion, be divided into two parts—a statement of the observed facts, and an explanation of the origin of the phenomena.

So far as it is a statement of facts, it cannot be called an hypothesis, for it simply affirms that the egg is optically an ordinary unspecialized cell; that it gives rise, during the process of segmentation, in a manner which is identical with ordinary growth by cell division, to a number of cells which gradually become specialized for certain functions, and are set apart as the foundations of the various organs of the body; that the repetition of this process gives rise, at last, to the perfect body of the mature animal; that the reproductive elements which are to give rise to the next generation, originate, like all the cells of the body, by cell division during the process of development, and that they are simply cells specialized for the reproductive function as other cells are specialized for other functions. Every one who has the slightest acquaintance with modern biology will accept this statement, not as an hypothesis, but as an observed fact, and will agree that between this and the old evolution hypothesis there can be but one choice.

The old hypothesis of evolution, however, claimed to be something more than a statement of fact, for the presence of the germ within the egg accounted for the wonderful properties of the egg itself.

We are at once compelled to ask, then, how, on the hypothesis of epigenesis, has the egg acquired these properties? If it is simply an unspecialized cell; if, as Gegenbauer states, "the egg is nothing more nor less than a cell; the egg-cell does not differ from other cells in any essential points" (Comp. Anat., Bell's Trans., p. 18), how can the egg of a horse develop into a horse, while another cell, which "does not differ from it in any essential points," develops into a bee or an alligator or an oyster?

Nothing in nature is more marvellous than the devel-

opment of each egg into its proper organism, and if it is true that the egg which is to give rise to a man differs in no essential point from that which is to give rise to an insect, we may conclude that the mystery is too great to be fathomed by our intelligence, and we may fairly ask what possible explanation can, on this hypothesis, be given of the wonderful properties of the egg.

The answer which has been given, and which seems to have been thought satisfactory by many students, is this:

We know, from a mass of evidence which is constantly and rapidly increasing, and to which each new observation adds cumulative weight, that the various forms of life have been slowly evolved, during long ages, from older and simpler forms; that as we trace back the history of any two animals or plants we find evidence that in the past they had for a common ancestor a species which had not yet acquired the distinctive features of either of them; that a little farther back we trace this species to an ancestor with still wider relationships.

Every day the evidence grows stronger to show that more complete knowledge will ultimately prove that the same thing is true of still larger groups; that families, classes and orders of organisms have been formed in the same way by gradual modification and divergence; that complete knowledge of the ancestry of any organism would lead us back through simpler and simpler forms to a remote unspecialized unicellular ancestral form. It is unnecessary to review in this place the evidence for this conclusion, for the fact that it is fully accepted by those best qualified to judge of its truth, is perfectly familiar to all students.

Now it is said, and the explanation is pretty generally accepted, that since any particular organism, a horse for

instance, has been slowly evolved from an ancestral rhizopod, and since the ovum of a horse is homologous with a rhizopod, or is morphologically equivalent to it, we have in the gradual phylogenetic evolution of the horse species from an unicellular ancestor, a satisfactory explanation of the ontogenetic development of the individual horse from an unicellular ovum.

As soon as attention is fairly fixed upon the subject, the weakness of this explanation becomes so evident that I take the liberty of making the following quotation from a well-known authority, in order to show that the explanation has been soberly advanced. In making the extract from Haeckel's writings I am not actuated by a desire to attack his views, for the same idea can be found, expressed pretty definitely, in the works of many other writers, and this particular selection is simply a matter of convenience.

Haeckel says: "Until recently the greatest students of embryology, Wolff, Baer, Remack, Schleiden and the whole school of embryology founded by them, have regarded the science as exclusively the study of individual development. Far otherwise to-day, when the mysteries of the wonderful history of the development of individual organisms no longer face us as an incomprehensible riddle, but have clearly revealed their deep significance: for the changes of form which the germ passes through under our eyes in a short time are, by the law of inheritance, a condensed and shortened repetition of the corresponding changes of form which the ancestors of the organism in question have passed through in the course of many million years. To-day, when we lay a hen's egg in an incubator, and in twenty-one days see the chick break out of it, we no longer gaze in dumb wonder on the marvellous changes which lead from the simple egg

to the two-layered gastrula: from this to the worm-like and skulless germ, and from this to later stages which repeat, essentially, the organization of fish, amphibian, reptile, until at last we have a perfect bird. On the contrary, we unravel from this history the corresponding series of ancestral forms, which have led up through the amœba, the gastræa, the worms, the acrania, the fishes, the amphibia and the reptiles to the bird.

"The series of changes in the hen's egg gives us an outline sketch of the series of ancestors. *This ancestral or phylogenetic significance of the phenomena of ontogeny or individual development is up to the present time the only explanation of the latter.*" ("Gesammelte Populäre Vorträge," II., p. 103.) "Any one who accepts the law that individual development is a recapitulation of the evolution of the species *will find it simply natural* that the microcosm of the ontogenetic cell-tree should be the diminutive, and in part distorted, reflection of the macrocosm of the phylogenetic genealogical tree of the species." ("Gesammelte Populäre Vorträge," II., p. 68.)

No one can set too high a value upon the scientific law here expressed—that individual development is a recapitulation of the history of the evolution of the species. It must be regarded as one of the greatest generalizations of modern science, but I do not think it is possible to agree with Haeckel that with its discovery the mystery of individual development has clearly revealed its deep significance, and no longer faces us as a riddle.

It may be true that it is "simply natural" that the egg of a horse should recapitulate the ancestral history of horses, and the egg of a bird the ancestral history of birds, but the statement that this is the case is in no sense an explanation of heredity. For that matter it is

"simply natural" that a bird's egg should give rise to a bird, and a horse-ovum to a horse, but no one would accept the statement as an explanation.

We have in the natural selection of variations a true *explanation* of the manner in which an unicellular rhizopod has been slowly and gradually modified by an almost infinite number of slight changes, extending through countless millions of generations, into a bird. The change is one of the most wonderful of the phenomena of nature, but it is in no sense a mystery, for the skill of the breeder may even now, by the employment of the same means, produce similar results, only on a much smaller scale; by the methodical selection of congenital variations an organism may be, in a few generations, slightly modified in any desired direction, and we can fairly and truly affirm that we understand the evolution of birds from their unicellular ancestors; but the resemblance between the evolution of birds from these remote ancestors by natural selection, and the development of an individual bird from an unicellular ovum, is simply an analogy. It is true that it is an analogy of the greatest significance, but we must not lose sight of the fact that the means by which the end is accomplished—the natural selection, through a long series of generations, of congenital variations—is absent in the second case. If the epigenesis hypothesis is true, if the egg is simply, like the rhizopod, an unspecialized cell; if the egg of a bird does not differ from the egg of a star-fish in any essential points, we must acknowledge that the mystery of individual development is not only as yet unsolved, but absolutely insoluble.

The student at the sea-shore may collect at the surface, with his dip-net, three similar transparent spherical eggs. Each of these is, optically, simply a nucleated

cell, and each when placed under the microscope will soon be seen to pass through almost exactly the same changes, giving rise by division to a spherical layer of cells. Yet if these three eggs are placed together in a tumbler of water and exposed to identical conditions, one may at last become a star-fish, another a crustacean, and another a vertebrate. Similar things under similar conditions cannot give rise to widely different results, and there seems no escape from the conclusion that these three eggs are not similar, or even essentially alike, but that one of them is a potential star-fish, another a potential crustacean, and a third a potential vertebrate. That there is in each of them a something which separates it very widely from the other two, and determines its future history.

The hypothesis of epigenesis proves, then, on careful analysis to be as unsatisfactory as the speculations of Bonnet and Buffon, and we must acknowledge that we are as yet unable to picture to ourselves the hidden significance of the phenomena of individual development, without returning to some modification of the old evolution hypothesis.

The attempt to escape this necessity, and to hold fast to the hypothesis of epigenesis, has given rise within recent years to much ingenious speculation, and an examination of some of the published papers will help, rather than retard, our argument.

Among these, one of the most ingenious and suggestive is Haeckel's paper, "Ueber die Wellenzeugung der Lebenstheilchen oder die Perigenesis der Plastidule." The following extract ("Gesammelte Populäre Vorträge," II., pp. 66–72) will, I hope, give a sufficiently clear statement of his views:

"In order to penetrate still farther into the mechan-

ics of the biogenetic process, we must descend into the deep obscurity of plastid-life, and search for its true efficient cause in the motion of organic molecules (Plastidule-Bewegung).

"In fine, this question remains to be answered, Are we in a position, by the aid of comparison with analogous phenomena of motion, to form a satisfactory provisional hypothesis regarding the true nature of the plastidule motions which are hidden from our direct observation? Our hypothesis of perigenesis is an attempt to answer this question in the affirmative.

"As we review, from the highest and most comprehensive point of view, the sum of the phenomena of organic development, the most general result of our survey is the conclusion that the biogenetic process is a periodic motion, which we can best picture to ourselves as a wave motion. Adhering at first to facts which are beyond dispute, and which admit of direct observation, we may commence with our own ancestry: either confining ourselves to the so-called historic period, in which we can pass from man to man by direct proof; or else following, by the methods of anthropogeny, our ancestry still farther back, through the vertebrates to amphioxus, and through the group of invertebrates to the gastræa, and at last to the amœba and the moner. In either case the course of development (entwickelungsbewegung) of our series of ancestors can be most simply represented by a wave-line, in which the individual life of each organism answers to a single wave.

"If now we enlarge our field of view to embrace not simply our own direct ancestry but the whole of our blood-relations, we can make clear by a genealogical tree their relationship to each other. As the history of the

evolution of each person is represented by a wave-line, the entire tree will have the form of a branched wave-motion, a ramified undulation. . . .

"A natural system of classification is nothing but a genealogical tree of allied species of organisms, and each branch and twig of the tree corresponds to a greater or smaller group of descendants from a common ancestral form. This community of descent unites all the forms of a class, an order, and so on. Since each class is divided into various orders, each order into several families, each family again into various genera, each genus into a number of species and varieties, there is a similar branching in the wave-motion which is carried from the common ancestral form to the entire group of its descendants; and each undulating branch implants in the same way its individual motion on its various descendants.

"Now the fundamental law of embryology teaches us that this history of the philogenetic evolution of organisms is mirrored in miniature in the ontogenetic development of each individual. Here the single waves answer to the life of the constituent plastids (cytodes and cells). The cytula, or the first segmentation cell which originates from the fertilized egg, and out of which the many-celled organism is developed, bears the same relation to the various cell-generations which originate from it by division, and which give rise later by specialization of function to the various tissues, that the stem-form of a class or order bears to the various families, genera and species which diverge from it, and which have been differently evolved through adaptation to diversified conditions of existence.

"The ontogenetic 'cell-tree' of the former has exactly the same form as the philogenetic 'species-tree' of the

latter. The developing impulse which in the one case is transferred from the ancestral species to the entire group of species, and in the other case from the ancestral cell to the entire group of cells, assumes in both cases the same form of a branching wave-motion. Any one who accepts the fundamental law of development will find it only natural that the microcosm of the ontogenetic 'cell-tree' should be a diminution, and to some degree distorted reflection of the phylogenetic 'species-tree.'

"As we can only explain and render intelligible a complicated and obscure phenomenon by dividing it into its separate elements, and by the exact analysis of these parts, so it is necessary to penetrate to the ultimate elementary facts of our mechanical theory of development.

"Now the biogenetic process as a whole is the highly compound resultant of the developmental history of all species of organisms. These consist again of the life histories of the individuals, just as the latter are again made up of that of the constituent plastids.

"The development of each plastid, however, is in its turn only the product of the active movements of its constituent plastidules. Now we have seen that the developmental impulse of the branches and classes, the orders and families, the genera and species, the individuals and plastids, always and everywhere has for its fundimental characteristics the branched wave-motion. Accordingly the molecular plastidule-motion, which lies at the bottom of all the phenomena of life, can have no other form. We must conclude that this ultimate cause of all the phenomena of life, that the invisible activity of the organic molecules is a branched wave-motion. This true and ultimate *causa efficiens* of the biogenetic

process I propose to designate by a single word—*Perigenesis,* the periodic wave-generation of the organic molecules or plastidules.

"This mechanical hypothesis is a true explanation of the process of organic development. . . .

"The designation of this branched wave-motion of the plastidule by the word *perigenesis* or *wave generation* serves to emphasize the distinctive characteristic which separates this *branched* motion from all similar periodic phenomena. This peculiarity depends upon the reproductive power of the plastidule, and this again is brought about by its peculiar atomic composition. This power of reproduction which alone renders possible the multiplication of the plastids is, however, the equivalent of the *memory* (Gedächtness) of the plastidule.

"This brings us to Ewald Hering's ably established view that unconscious memory is the most important characteristic of organized matter, or more properly of the organizing plastidules. Memory is the chief factor in the process of development of organisms. Through the memory of the plastidules the plasson has the power to carry over from generation to generation by inheritance, in continuous periodic motion, its characteristic peculiarities, and to add to these the new experiences which the plastidules have acquired through adaptation in the course of their evolution.

"I have shown that each organic form is the necessary product of two mechanical factors—an inner factor, heredity, and an outer factor, variability, or a power of adaptation.

"By the hypothesis of perigenesis we are able to more sharply define these two fundamental laws of the modification of organisms, for *heredity is the memory of the plastidules: variability their power of perception* (Die

Erblichkeit ist das Gedächtniss der Plastidule, die Variabilität is die Fassungskraft der Plastidule). The one brings about the constancy and the other the diversity of organic forms. In the very simple and persistent forms of life the plastidules have, so to speak, learned nothing and forgotten nothing. In highly perfected and variable organisms the plastidules have both learned and forgotten much."

This somewhat long quotation contains a thorough and exhaustive statement of the perigenesis hypothesis, and it is therefore interesting to notice that its only real claim to recognition as a true *explanation* of the phenomena of heredity is based upon or at least demands the acceptance of some form of the evolution hypothesis.

However great may be the importance of the analogy between the gradual evolution of the species by the specialization of the constituent individuals, and the development of the individual by the specialization of cells, and plastidules, we have already pointed out that it is in no sense an explanation of the latter, since the real cause of the evolution of the species, the selection of congenital variations, is absent.

The only part of Haeckel's hypothesis of perigenesis which has any claim to be considered an explanation of the reproductive power of animals, is the statement that heredity is memory, and variability the acquisition of new experiences. Stated by itself, without explanation, this may seem to those who are unfamiliar with the subject very much like nonsense, for the profound truth upon which it rests is not at all obvious at first sight.

Herbert Spencer has, in his masterly discussion of the nature and distinctive characteristic of life, given us, as the sum and substance of his analysis, the statement

that "life is the continuous adjustment between internal relations and external relations." This, like Haeckel's statement that heredity is memory, is not very clear without explanation, but its meaning may perhaps be brought out by an illustration.

If I kick a stone I produce in it certain changes, such as motion, heat, etc.; these changes being directly produced by the kick are simply manifestations of the energy transferred from my foot to the stone. If, instead of a stone, I kick a dog, I produce a similar set of changes, and something more. The experience of the dog and of his ancestors has taught him that such violent attacks are always associated with a disposition to commit still further violence, so, when the dog feels the blow he immediately performs actions which have as their object, escape from or avoidance of the danger which he has not yet experienced, but which he knows to be imminent. These actions are not the effect of the kick, for the energy expended may be hundreds of times greater. Their character is determined, not by any change in the dog, but by the character, the disposition, which he has inherited; and whether he retaliates by an attack on his own part, puts his tail between his legs and runs, or crouches at my feet, his actions are the effect, not of the kick, but of past experience as to the best means of escaping further injury. There is a relation, external to the dog, between the kick and a disposition to injure the dog, and there is within the dog a relation between the sensation of injury and the actions which experience has shown to be the proper ones for escaping further injury.

That which distinguishes the dog from the stone is the power to adjust these internal relations to the external relations, to conform his conduct to the laws of

the world around him. The dog, as a living thing, differs from all inorganic bodies, in his power to make this adjustment: so long as he retains this power he lives; his life is a "continuous adjustment between internal relations and external relations." It is plain that this power depends upon experience, but experience depends upon "memory." So we may state, with truth, that in a certain sense, life is memory; and as the power to reproduce its like is characteristic of all living things, we see that there is in Haeckel's statement a profound truth.

We know memory, however, only in connection with organization, and if it is true that heredity, the power of an organism to reproduce its like, is simply the memory, by the ovum, of the experience of its ancestors, we must believe that there exists in the ovum an organization of some kind to correspond to each of these past experiences.

We are therefore driven by the hypothesis of perigenesis back from the hypothesis of epigenesis to some form of the old evolution hypothesis, for we cannot conceive that complicated experiences should exist without complicated structure.

We are thus compelled to conclude that, while it undoubtedly expresses a great truth, Haeckel's hypothesis of perigenesis is not a satisfactory and final explanation of the phenomena of reproduction. A satisfactory theory of heredity must explain what it is, in the structure and organization of the ovum, which determines that each ovum should produce its proper organism.

To state that this organization can be expressed in terms of memory, is simply to state the familiar truth that matter and force are different aspects of the same thing; that all problems of matter may be put into the

terms of force. The statement does not help us at all to picture to ourselves the essential hidden structure of the egg, the organization upon which its wonderful properties depend.

Jäger has recently brought forward an hypothesis which seems at first sight to be a satisfactory epigenesis hypothesis, but examination shows that this too, like Haeckel's perigenesis hypothesis, must be turned into an evolution hypothesis before it can be accepted.

The following extract from his paper ("Zur Pangenesis," von Prof. Dr. C. Jäger. *Kosmos* iv. 376. 1879) gives, I believe, a fair statement of his views.

"Each organ and tissue of an animal or plant contains, in the molecules of its albumen at least, a specific *flavor-and-odor-substance* (Duft-und-Würzestoff) which we can easily recognize by our chemical sense, for each organ of an animal has its distinctive flavor. Whenever a full-grown animal experiences hunger, decomposition of albumen takes place in all its organs and tissues, so that their various *flavor-and-odor-substances*, that is their soul-substance (Sezenstoffe), become free, and penetrate to all parts of the body.

"Now, if there exists in any part of the body protoplasm with the power to attract this substance, this protoplasm acquires in this way its *vires formativæ.*

"I have already referred with emphasis to the embryological fact that the formation of the reproductive elements takes place at a very early stage in the embryonic life of an animal, and I have designated this as the reservation of germinal protoplasm. As soon as the embryonal cells of the developing animal have become specialized into ontogenitic and phylogenetic cells, the following will occur. Whenever any decomposition of albumen occurs in the developing organism, from hun-

ger or any other cause, the ontogenetic cell-material which builds up the organism will set free soul-stuff.

"By the law of gaseous diffusion this will not only escape from the body as an excretion, but it will also penetrate to the germinal or phylogenetic protoplasm. This process I shall now term soul-reception (Seelenfängerei) in the following sense. The chemical substance which forms the greater part of the ova and male cells has lately been called nuclein, since it shows the closest resemblance to the cell-nucleus. The yolk-substance is now regarded, not as vitellin, but egg-nuclein, and the substance of the male cell not spermatin but sperm-nuclein. We also know that nuclein consists of albumin, and phosphoric lecithin.

"The question then is the origin of the nuclein in the egg, and the male cell, and this may be answered as follows:

"The reproductive organs do not receive albumen from the body of the mother, since according to the law of Traube, the molecules of a substance which forms a membrane cannot, on account of their size, pass through the pores of that membrane. The germ-cell is an albuminous membrane, and hence it will not allow the passage of albumin molecules.

"It simply contains the albumin-nucleus, which remains after the decomposition of the soul-substance, and this is a peptone-like substance which, having lost its soul-substance, has a smaller molecule. It is therefore unspecialized, or deprived of its soul (entspesificirt, entseelt), and the process of assimilation in the germ may be termed soul-restoration (Wiederbeseelung). The necessary soul-substance is supplied by the decomposition of albumen in the ontogenetic cell-material.

"Thus, for example (p. 380), it is known that the re-

productive organs of a caterpillar are already formed before it leaves the egg. During its life in the egg, and as a caterpillar, caterpillar-nuclein is formed in its germinal cell-material. During the pupa stage pupa-nuclein is stored up in its reproductive elements, and finally, when it becomes a butterfly, butterfly-nuclein is stored up. The ripe egg and the ripe male cell therefore contain nuclein of three kinds, caterpillar-nuclein, pupa-nuclein, and butterfly-nuclein."

It will be seen that Jäger's hypothesis is, in a certain sense midway between evolution and epigenesis. He holds that at first both the ovum and the male-cell are unspecialized (entseelt); that they exist in the very young embryo as embryonic ova or spermatozoa, and that, as the embryo grows up, the reproductive cells gradually become specialized by the assimilation of soul-stuff, which is thrown off by the decomposition of albumen in various parts of the body of the growing organism, and penetrating to the embryonic ova and spermatozoa is assimilated by them, so that when the animal becomes sexually mature, the cells of its reproductive organs contain all the "soul-stuff" necessary to produce a new organism like the parent.

The statement which I have given is a free translation of Jäger's outline of his theory, and I think it may be regarded as a fair exposition of his views.

A fatal objection to his hypothesis is found in the fact that where a parent gives birth to young before it has reached full maturity and before it has acquired all the characteristics of the species, the young nevertheless inherit these characteristics. The young which are born by a Cycedomia larva inherit all the characteristics of the full-grown adult insect, and a bull may transmit to female children the good milking qualities of his

mother. It is plain that the child of a beardless boy could not inherit the "soul-stuff" of a beard in the way Jäger imagines, and this fact alone is enough to show that he has not discovered the true secret of heredity.

We know, too, that reversion, the appearance in the child of the features inherited from a remote ancestor but not shared by its parents, is not at all unusual, and must be regarded as one of the leading characteristics of heredity. It is plain that if the embryonic ovum is, as Jäger states, unspecialized or "de-souled," reversion is inexplicable. Accordingly, when he comes to discuss reversion he makes a fundamental change in his hypothesis, and holds that when the ovum divides, at a very early stage of its development, into two parts, an ontogenetic portion, which gives rise to the new organism, and a phylogenetic portion, which ultimately forms the germinative cells of its reproductive organ, the second part is not unspecialized or "de-souled" at all, but really retains all the characteristics of the ovum which gives rise to it, and is therefore capable, like the ovum, of giving rise to a new organism.

As thus remodelled, I believe, and hope to show in the sequel, that Jäger's hypothesis is a close approximation to the truth, but it is only fair to point out that in its altered form it is not original with Jäger. The author published almost exactly the same view in 1876 ("On a Provisional Hypothesis of Pangenesis," *Proc. Amer. Assn.*, 1876, and *American Naturalist, March*, 1877), and it had been stated as long ago as 1849 by Prof. Owen, in his paper on Parthenogenesis, although this author, in his "Anatomy of Vertebrates," afterwards states that he now believes it to be fundamentally erroneous. It is plain, too, that in its second form Jäger's hypothesis is one of evolution, pure and simple,

for the egg is, at no stage of its growth, unspecialized, and it does not require the assimilation of "soul-stuff" in order to develop into an organism.

We must conclude, then, that however satisfactory and accordant with observed fact the hypothesis of epigenesis seems to be at first sight, more careful analysis shows that it is in no sense a true explanation of the phenomenon of development.

The analogy between the evolution of the species from an unicellular ancestor, and the development of the individual from an unicellular egg, is simply an analogy, for the cause of the first phenomenon, the selection of congenital variations, is wanting in the second case, and there is nothing to take its place if it is true that an egg is really, like a rhizopod, an unspecialized cell.

Haeckel's statement that heredity is memory, however true it may be, cannot be accepted as an explanation, for we have no knowledge of the existence of memory apart from organization, and we cannot conceive that an ovum can retain the memory of the past history of its species, unless it possesses a corresponding organization.

Jäger's view that the embryonic ovum is unspecialized, and that its specialization is gradually assimilated during the development of the organism which contains it, fails to account for the phenomena of reversion, and to account for reversion he is compelled to assume that the egg is organized from the time of its origin in the developing egg of the preceding generation.

In each case we are driven to the same conclusion, that the epigenesis hypothesis is inadequate, and we are forced to accept some form of the evolution hypothesis.

This necessity has not escaped the notice of some of our most acute thinkers. Huxley, for example, says

(Encyc. Brit., Art. Evolution), "Harvey's definition of a germ as 'matter potentially alive, and having within itself the tendency to assume a definite living form,' appears to meet all the requirements of modern science. For notwithstanding it might be justly questioned whether a germ is not merely potentially but rather actually alive, though its vital manifestations are reduced to a minimum, the term potential may fairly be used in a sense broad enough to escape the objection. And the qualification of potential has the advantage of reminding us that the great characteristic of the germ is not so much what it is, but what it may under suitable conditions become. "From this point of view the process, which in its superficial aspects is epigenesis, appears in essence to be evolution, . . . and development is merely the expansion of a potential organism or organic preformation according to fixed laws."

CHAPTER III.

HISTORY OF THE THEORY OF HEREDITY—(*Continued*).

Some form of the evolution hypothesis a logical necessity—Darwin's pangenesis hypothesis—This is an evolution hypothesis, since all the characteristics of the adult are supposed to be latent in the germ—Miscellaneous objections to it—These objections do not show that it conflicts with fact—Difficulty in imagining detailed working is no reason for rejecting it—Galton's experimental disproof—There are many reasons for believing that the sexual elements have different functions—The evidence from parthenogenesis—Polar-cell hypothesis—The evidence from hybrids, from variation, and from structures confined to one sex—The pangenesis hypothesis recognizes no such difference in the functions of the reproductive elements—We must therefore distrust its absolute correctness—Summary of last two chapters.

Some Form of the Evolution Hypothesis a Logical Necessity.

Most of the hypotheses which have been proposed, of late years, to account for the phenomena of heredity, are like the two we have quoted, epigenesis hypothesis, for they are attempts to show that the ovum is in reality, as well as in form, an unspecialized cell. Analysis shows, however, that they all rest ultimately upon the assumption that this is not true, but that the ovum really contains, in some form or other, actually or potentially, the future organism, with all its hereditary characteristics.

We know that eggs which are to all appearances essentially alike, may, when artificially removed from the ova-

ries and artificially fertilized, and when kept under exactly the same conditions, develop into widely different organisms, and as like things cannot, under like conditions, give rise to different results, we are forced to conclude that these eggs are not essentially alike, but that each contains within itself in some form the organism to which it is to give rise—that individual development is, in some sense, the unfolding of a germ which already exists in the egg. There is no escape from this conclusion, at least there is none which can be accepted by the scientific student, and we see that logical thinkers like Prof. Huxley are driven to conclude that the process which in its superficial aspects is epigenesis, appears in essence to be evolution.

Darwin's Hypothesis of Pangenesis.

In contrast to the views already quoted we have the well-known pangenesis hypothesis of Darwin, an hypothesis which is thoroughly one of evolution, since Darwin believes that the whole organization of the species is present not only in the egg but in the male cell also; that each of these not only contains the complete organization of the parent, but an indefinite series of similar organizations, inherited from a long line of ancestors. It is true that Darwin does not believe that each of these ancestors is represented in the ovum and in the male cell by a minute but perfect animal, like those imagined by Bonnet, but he imagines what is essentially the same thing, that each of the cells of each parent, and every cell of each ancestor for a long and practically an unlimited series of generations, is represented in each ovum and each male cell by a germ capable of producing that particular cell with all its distinctive characteristics.

Darwin's original statement (*Variation,* chaps. xxvii.

and xxviii.) is readily accessible, but it will not be out of place to quote it before entering upon its critical discussion.

He says: "In the previous chapters large classes of facts, such as those bearing on bud-variation, the various forms of inheritance, the causes and laws of variation, have been discussed, and it is obvious that these subjects, as well as the several modes of reproduction, stand in some sort of relation to each other. I have been led, or rather forced, to form a view, which to a certain extent connects these facts by a tangible method. Every one would wish to explain to himself, even in an imperfect manner, how it is possible for a character possessed by some remote ancestor suddenly to reappear in the offspring; how the effects of increased use or disuse of a limb can be transmitted to the child; how the male sexual element can act not solely on the ovule, but occasionally on the mother form; how a limb can be reproduced on the exact line of amputation, with neither too much nor too little added; how the various forms of reproduction are connected, and so forth. I am aware that my view is merely a provisional hypothesis or speculation, but until a better one be advanced it may be serviceable by bringing together a multitude of facts which are at present left disconnected by any efficient cause. As Whewell, the historian of the inductive sciences, remarks, hypotheses may often be of service to science, when they involve a certain portion of incompleteness or even of error.

"Under this point of view I venture to advance the hypothesis of pangenesis, which implies that the whole organization, in the sense of every separate atom or unit, reproduces itself. Hence ovules and pollen grains—the fertilized seed or egg, as well as buds—include and con-

sist of a multitude of germs thrown off from each separate atom of the organism."

From the extract we see that the hypothesis is an attempt to show that all the phenomena of generation and development, including those of variation as well as those of heredity, depend upon the fact that each structural unit of the body is the direct offspring of a similar unit in the body of a parent or of a more remote ancestor. The cells of the body of one of the higher organisms are not only morphologically but actually independent individuals, reproducing themselves directly in the next generation: and the germ of such an organism is in reality an aggregate of these cell-germs.

Stated more at length, the hypothesis is as follows:

"I assume that cells, before their conversion into 'form material,' throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment, multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules, for the sake of distinctness, may be called . . . gemmules. They are supposed to be transmitted from the parent to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules, which precede them in the regular order of growth. Why I use the term union will be seen when we discuss the direct action of pollen on the tissues of the mother plant.

"Gemmules are supposed to be thrown off by every cell or unit not only during the adult state but during all stages of development. Lastly I assume that gemmules

in their dormant state have a mutual affinity for each other, leading to their aggregation either into buds or into the sexual elements. Hence, speaking strictly, it is not the reproductive elements nor the buds which generate new organisms, but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis of pangenesis."

Darwin's gemmules are, of course, entirely imaginary, that is, a belief in their existence does not rest upon direct observation. We cannot deny that the hypothesis furnishes an explanation of most of the phenomena which he attempts to interpret by it, although it seems possible that there may be a simpler explanation. If the existence of the gemmules were proven we could understand not only the wonderful facts of ordinary inheritance by sexual reproduction, but the various forms of asexual reproduction as well.

We should have a simple explanation of the manner in which the characteristics of a remote ancestor may suddenly reappear after they have been dormant for many generations. We should understand how the embryological history of a species may become simplified by the omission of larval forms or appendages. In a word, nearly all the phenomena of heredity admit of explanation by the hypothesis, and those who have criticised it have not usually attempted to show that it conflicts with fact, but have simply objected to it as a purely imaginary explanation. It is urged that the transmission of all the characteristics which we know to be inherited from near and remote ancestors demands that the number of gemmules should be almost unlimited and practically infinite; that not only are the gemmules imaginary, but that the aggregation of such numbers in masses as small as the reproductive elements requires

that they shall be of inconceivable minuteness, and that nature furnishes no analogy for attributing to such small particles the vital properties which we know only in bodies which are comparatively gigantic. It is also urged that the gemmules must be endowed with entirely imaginary and wonderfully specialized elective affinities, in virtue of which each develops only at the proper time and place. In order to account for the manner in which the characteristics of each parent are mingled in the child we must regard each individual as the product of a struggle for existence among the gemmules, resulting in the selection and development of the fittest. The formation of several individuals asexually by budding from a parent stock demands that the gemmules themselves must be capable of multiplication, and that they must have the power to transmit their properties to their offspring. To explain alternation of generations we must suppose that the embryo receives several complete sets of gemmules, which are not duplicates, and it is almost impossible to follow out, in thought, the complicated relations which must exist between the gemmules of the egg-embryo of such an organism as a Siphonophore.

These and similar objections may be fairly urged, and while their great weight is obvious, we must not attach undue importance to them, for they do not show that the hypothesis conflicts with any known law or observed fact, and the great drafts made upon the imagination should not, alone, prevent its provisional acceptance so long as we have no simple explanation of the phenomena, for difficulty in imagining the details of an hypothesis is a purely subjective matter, which varies with the age and with the individual.

Galton's Experiments.

Besides these theoretical objections, we have the experimental disproof furnished by Galton. In order to test the hypothesis this experimenter selected the silver-gray rabbit—a variety which has, in itself, little tendency to vary, although it readily crosses with other varieties, and breeding freely with them gives birth to hybrid offspring. Into the bodies of eighteen of these silver-gray rabbits he transfused the blood of other varieties, in some cases replacing one half of the blood. From the eighteen rabbits thus operated upon eighty-six young were produced, and in no case did the offspring exhibit any of the characteristics of the variety from which the blood was taken, but all of the eighty-six were pure silver gray. From these experiments Galton concludes that "the doctrine of pangenesis, pure and simple, is incorrect;" and I think we must agree with him that this conclusion is justified by the results which he reached, although I hope to show that it is possible to restate the hypothesis in a form which is so modified as to escape this objection.

The Sexual Elements Perform Different Functions in Heredity.

There is another objection which seems to me to be of almost equal weight, but which has never, so far as I am aware, been pointed out. The early writers upon heredity attributed certain functions to the male cell and others to the ovum; but we now know that their means of observation were so inadequate, and their knowledge so limited, that their conclusions were of little value, and that both ovists and spermists were wide of the mark. The fact that they erroneously attrib-

uted certain functions to the ovum and certain others to the male cell does not, of course, prove that there is no difference in the functions of these elements; but in modern times we actually find that thinkers have gone to this opposite extremity of the subject, and have either tacitly implied or directly accepted the view that the two sexual elements play similar parts in heredity.

Neither Haeckel's hypothesis nor Jäger's recognizes any difference in their functions, while Jäger seems to believe, and Darwin explicitly states, that their shares in hereditary transmission are alike.

Many facts indicate that this view is, to say the least, very improbable, and I will give, briefly, a statement of some of the arguments against it, and will then devote a little space to a discussion of the reasons which have been given by Darwin and others for accepting it.

The structural difference between the ovum and the male cell is one of the most widespread and fundamental characteristics of organic beings, and it is found in all except the very lowest animals and plants. It is, to say the least, very improbable that a structural difference so fundamental and so nearly universal should have no functional significance, and the fact that in many marine animals, when the ripe unfertilized ova are thrown out into the ocean, like the male fluid, to be swept away by the tide, the sexual elements differ in the same way that they do in animals whose eggs are fertilized inside the body of the female, forbids us to believe that the difference depends simply upon the fact that the male cell must make its way to the ovum.

Many of the secondary characteristics of the ovum, such as its great size in birds and reptiles, and the presence in it of food-material in so many animals, are no

doubt traceable to the fact that, in most animals, the egg is stationary, while the male cell can be conveyed from place to place; but we must believe that there is some more fundamental and primitive difference.

Even if the phenomena of Parthenogenesis did not show us that the part played by the ovum is more essential to the perpetuation of the race than the part played by the male cell, we should still be justified in the belief that the difference in form corresponds to some profound difference in function, and the possibility of Parthenogenesis shows beyond question that this is the case.

Parthenogenesis.

Siebold has proposed the term parthenogenesis for the power which is possessed by certain female animals, especially the arthropods, to produce descendants without sexual union with a male.

The existence of this power was first pointed out by Aristotle (*De Generatione Animalium, Lib. III., Cap.* 10, 21, 22, 23). As this remarkable observer had no means for exact research at his command, he was, of course, unable to make use of rigid tests, or to furnish the severely exact proofs which have been given us by more modern naturalists; but he gives many reasons for suspecting that the unfertilized eggs of the honey-bee may give rise to perfect animals without sexual union; and although we now know that some of the reasons he urges do not really prove the case, yet modern science has given the most conclusive proofs of the correctness of his general conclusion.

I shall devote considerable space to this subject in order to show the unscientific reader that the existence of fertile virgin female animals is proved by the obser-

vations of a great number of competent naturalists; that the subject has been thoroughly and carefully studied, with every precaution against error, and that our belief in its existence does not rest upon the unverified statements of a few observers.

In this summary I shall give many references to authorities, but as my purpose is not to give a complete bibliography, but simply to show how thoroughly the subject has been studied, many names are omitted.

Most of the following facts are taken from Gerstecker's history of the subject in Volume v. of Bronn's *Klassen und Ordnungen des Theirreichs,* although I have referred to many of the original papers and have added many facts which are not mentioned by Gerstecker. The subject is perfectly familiar to most naturalists, and the amount of space devoted to it may seem unnecessarily great to such persons, but it is important to impress upon unscientific readers a sense of the exact and definite character of the evidence for the existence of parthenogenesis, and a short history of the subject seems the most effective means for accomplishing this purpose.

Among the crustacea and insects, parthenogenesis is by no means unusual. It occurs in some groups where impregnation by males is so nearly universal that naturalists have been slow to credit any exceptions. In other groups it is the general rule, and fertilization by a male is the exception. In some genera and species the power is shown only by a few individuals, while in others it is shared by all the females. In some cases the unfertilized eggs give rise to females only, in other cases to males, and in still other cases to both sexes.

In 1775, Schäffer, of Regensburg, discovered its occurrence in fresh-water crustacea, although Dr. Albrecht

had made the same discovery in insects in 1701. Schäffer found ("Abhandlungen von Insecten") that when a female specimen of the common water-flea or *Daphnia,* a small fresh-water crustacean, is placed by itself immediately after it is born, and is kept throughout its whole life without any chance of union with a male, it gives birth to great numbers of young females, and that the isolation of these young specimens has no more effect upon their fertility than it had in the case of their mother, but that they continue to reproduce for an indefinite number of generations when all chance of access to a male is excluded.

This observation may be repeated by any one with the greatest ease, for Daphnia is very common in most fresh water ponds and streams, and it multiplies in confinement with great rapidity, so that there is no difficulty in verifying Schäffer's experiments, or in showing the correctness of his conclusions.

Certain authors have held that the parthenogenetic eggs of Daphnia are not true eggs at all, but simply internal buds (Lubbock, *Phil. Trans.*, 147, p. 88), and that the so-called "winter eggs," which seem, in most cases at least, to require impregnation, are the true ova; but Weissmann, who has made a very thorough study of the origin of the ova in the ovary of Leptodora ("Ueber die Bildung von Wintereiern bei Leptodora hyalina," *Zeit. f. Wiss. Zool.*, xxxv.), has shown that while there are some minor differences in the mode of origin of the two kinds of eggs, both are real ova in the strictest sense, and cannot be compared with buds.

Schäffer's experiments were independently repeated in 1820 by Jurine, and this observer not only reached the same result, but also proved that fertile winter eggs

may be produced by isolated females whose mothers and grandmothers had been isolated all their lives.

Claus has shown that the eggs begin to develop in the female Evadne, a form closely related to Daphnia, before the animal is born ; and impregnation would here seem to be impossible.

In Daphnia and related forms the parthenogenetic eggs appear to give rise to females only, but as the males are very rare indeed, as compared with the females, it is difficult to show that they never originate by parthenogenesis, for the evidence is only negative. Schäffer, the discoverer of parthenogenesis in Daphnia, also discovered that Apus, a crustacean which belongs to another order, lays eggs which give rise without impregnation to fertile females, and that this may go on for an indefinite number of generations. In Apus, and in most of its allies, the males are extremely rare, although the females may be very abundant, and one observer, Joly, found only one male specimen of Artemia salina among 3000 females.

Parthenogenesis is known to occur in many insects. It is rare and exceptional in some of them, while in others it is as frequent and normal as it is in Daphnia.

Among the butterflies and moths, sexual union is the rule, and parthenogenesis a rare exception, but in 1701 Dr. Albrecht made the remarkable discovery that a female Bombyx, which had escaped from its pupa under a glass shade, and which could not have been visited by a male, laid fertile eggs. As sexual union is known to be almost universal in the Bombycidæ, this observation was at first discredited, but the phenomenon has in more modern times been observed with every possible precaution in Bombyx mori by a number of most competent observers, among whom are Schmidt, Barthél-

emy, Jourdan, Siebold and others. They all agree that while parthenogenesis is rare in this species, it does sometimes occur, and it is known that the parthenogenetic eggs give rise to fertile males and fertile females, which may unite sexually and thus produce fertile eggs. Dr. Kipp has reared another form, *Smerinthus populi*, from eggs fertilized by a male which hatched from a parthenogenetic egg, and laid by a female which had been reared in the same way.

In Bronn's *Klassen und Ordnungen*, Gaerstecker gives the following list of moths in which parthenogenesis has been observed, with the name of the observer. The list might be greatly enlarged by the addition of cases which have been recorded since its compilation, but it is sufficient for our purpose, which is simply to show that the fact has been verified repeatedly by many observers.

Sphinx ligustri, once..Treviranus.
Smerinthus populi, four times....Nordmann, Brown, Newnham, Kipp.
Smerinthus ocellatus, once................................Johnston.
Euprepia caja, five times....Brown, Lehocq, Robinson, Schlapp, Barthélemy.
Euprepia villica, once....................................Stowell.
Saturnia Polyphemus, twice..................Curtis, De Filippi.
Gastropacha pini, three times......Scopoli, Suckrow, Lacordaire.
Gastropacha quercifolia, once..............................Basler.
Gastropacha potatoria, once.........................Burmeister.
Gastropacha quercus, once............................Pleininger.
Liparis dispar, once...Carlier.
"Egger Moth" (Liparis dispar ?), once.......................Tardy.
Liparis ochropoda, once......................................Popoff.
Orgyia pudibunda, once...................................Wernberg.
Psyche apiformis, once...Rossi.
Bombyx mori, many times...........Schmidt, Siebold, Jourdan, Barthélemy, and others.

Although these cases make a long list, which might be greatly increased, they are still exceptional, for in all these species almost all the eggs fail to develop unless they are fertilized by a male; but in some other groups of insects parthenogenesis occurs more frequently, and seems to be perfectly normal. The most remarkable instances are those which occur in the social insects, such as the bees.

It is well known that a community of honey-bees consists of individuals of three kinds—the workers or rudimentary females, which are the most numerous; the perfect females or queens, of which only one is usually present in a hive; and the drones or males.

In the workers, or as they are sometimes falsely called the neuter bees, the female reproductive organs are very imperfectly developed: the vagina is so small that union with a male is hardly possible, and the receptaculum-seminis is very rudimentary, yet it is well known to all bee-cultivators that they do sometimes lay eggs which are capable of development, not only in the honey-bee but in other species also. Among the honey-bees such fertile workers are always found in a hive which has lost its queen, and they have been called "drone mothers," from the fact that their eggs produce only drones or males.

The queen-bee is the only member of the hive which unites sexually with the males, and her reproductive organs are very large and well developed, as contrasted with those of the worker. Her receptaculum-seminis is large enough to retain a sufficient supply of the male fluid to serve for fertilizing great numbers of eggs, and it is usually found to contain a considerable quantity. Sexual union takes place during flight, and queens with imperfect wings are never impregnated, and Siebold,

Leuckart, Berlepsch, and others have shown, by microscopic examination, that in such cases the receptaculum-seminis is empty, and the queen is a virgin. In such cases, as well as in hives, where the receptaculum-seminis of the queen has been exhausted by old age, or has been removed, it is well known to bee-cultivators that only drones are produced, while eggs destined to give rise to females, to workers or perfect queens, are produced only by queens which have been impregnated and have some of the male fluid in the receptacle. This fact, considered in connection with the fact that the eggs laid by workers produce only drones, indicates that the drone eggs laid by an impregnated queen are not fertilized; and Siebold has found active spermatozoa on newly laid worker-eggs, but has failed to find them on drone-eggs. We are, therefore, compelled to believe that the queen is able to lay both fertilized and parthenogenetic eggs. It is stated that when a queen of the common German variety is crossed with a drone of the Italian bee she produces hybrid workers, while her male offspring are all pure German bees.

In certain Lepidoptera, as in the bees, parthenogenesis seems to be normal, and it has been observed in Solenobia and Psyche by a great number of ancient and modern naturalists, including Schrank, Réaumer, Pallas, De Geer, Scriba, Speyer, Reutti, Siebold, Leuckart, Hofmann, and others. Their observations show—1st, that the wingless female is abundant and widely distributed at all seasons, while the winged males are seldom met with, and are found only in certain restricted localities; 2d, that there is only one form of female; those which unite with the male, as well as those who do not, have perfect reproductive organs which resemble those of other butterflies. Parthenogenesis is the rule, and the female

lay eggs as soon as they have passed through the pupa stage. These parthenogenetic eggs give rise only to females, and these may give rise to female descendants in the same way for an indefinite number of generations; 3d, in at least one species (*Solenobia triquetrella*), the eggs which are laid by impregnated females give rise to both sexes.

Dufur, Kessler, Hartig, Walsh, and many other naturalists have shown that certain female gall-wasps are parthenogenetic; within recent years Bassett and Adler have made most interesting observations upon these wasps. In 1873 Bassett showed (*Canadian Entomologist*, 1873–75, p. 91) that great numbers of male and female wasps escape in June from certain galls which are found in very great abundance on the leaves of an oak. Late in the summer the females lay their eggs in the leaves of the same oak, and give rise to galls, which, however, are of quite a different character from those in which the insects were born. Early in the following spring a brood of females hatch from these winter galls, and at once lay parthenogenetic eggs, which give rise to the summer galls, and hatch in June into males and females.

Bassett and Adler have extended these observations to a great number of species, and the following account is taken from a paper by the latter writer ("Ueber den Generationswechsel der Eichen-Gallwespen," von Dr. H. Adler, *Zeit. f. Wiss. Zool.*, xxxv. 151), who has carried on a long series of the most painstaking experiments, using every precaution against error.

He reared a great number of small oak-trees under glass cases, and then, introducing the wasps, traced their whole life history, and he found that in many species there is a winter gall, which is produced in the fall by a

fertilized female, and which gives rise early in the spring to a brood of females without males. These at once lay their eggs and form summer galls, from which both sexes are born.

In all cases the parthenogenetic forms are so different from the sexual forms that they had previously been described as distinct species, and in most cases they had been placed in distinct genera.

The following example selected from Adler's paper will give an idea of the character of his experiments: *Neuroterus lenticularis* is a wasp which is born within a small round gall which appears in July on the lower surfaces of oak leaves. The galls continue to grow until the end of September, when the leaves drop off and fall to the ground. In the spring the insects escape, and all of them are females, with their ovaries full of eggs, and the male of this species was unknown previously to Adler's experiments. He gathered the fallen leaves, and rearing the wasps in isolated captivity found that, soon after the female is born, she pierces the leaf buds of the oak, and lays her eggs. Adler marked by pieces of thread all the buds which the insect was actually seen to pierce, and in a few days he found on the leaves which expanded from these buds a great number of minute young galls, which soon became large enough to show that they were very different from the winter gall in which the parent was born.

This new gall proved to be one with which entomologists had long been familiar, as the birthplace of what had always been regarded as a wasp of quite a different genus—*Spathogaster baccarum.* It is a soft green gall, punctated with red spots, and it grows entirely through the leaf, so that part is on the upper and part on the lower surface. The oak trees with these galls were kept

carefully protected from the access of other insects until about the middle of June, when male and female specimens of *Spathogaster baccarum* were produced. The sexes united at once, and the females were then isolated and placed in captivity, each with its little oak tree. They soon laid their eggs in the leaf buds, and thus gave rise to the winter galls, which, in the following spring, produced a brood of the parthenogenetic female *Neuroterus lenticularis.*

He has made similar careful observations on many other species, and he gives the following table to exhibit his results:

Parthenogenetive form born from a winter gall, and producing a summer gall.	Sexual form born from a summer gall, and producing a winter gall.
Neuroterus lenticularis.	Spathogaster baccarum.
Neuroterus læviusculus.	Spathogaster albipes.
Neuroterus neumismatis.	Spathogaster vesicatrix.
Neuroterus fumipennis.	Spathogaster tricolor.
Aphilotrix radicis.	Andricus noduli.
Aphilotrix Sieboldi.	Andricus testaceipes.
Aphilotrix corticis.	Andricus gemmatus.
Aphilotrix globuli.	Andricus inflator.
Aphilotrix collaris.	Andricus currator.
Aphilotrix fecundatrix.	Andricus pilosus.
Aphilotrix callidoma.	Andricus cirratus.
Aphilotrix Malpighii.	Andricus nudus.
Aphilotrix autumnalis.	Andricus ramuli.
Dryophanta scutellaris.	Spathogaster Taschenbergi.
Dryophanta longiventris.	Spathogaster similis.
Dryophanta divisa.	Spathogaster verrucosus.
Biorhiza aptera.	Terus terminalis.
Biorhiza renum.	Trigonaspis crustalis.
Neuroterus ostreus.	Spathogaster aprilinus ?

In the following four species no males were discovered, but the parthenogenetic females gave birth to females like themselves:

Aphilothrix seminationis. Aphilothrix quadriliniatus.
Aphilothrix marginalis. Aphilothric albopunctata.

These are all of them insects which form galls on oak leaves, but Adler finds that the same power to lay parthenogenetic eggs exists in some other wasps. *Pteromalus puparum* lays its eggs in the bodies of butterfly larvæ, and thus gives birth to both males and females. The sexes are so different that there is no difficulty in separating them as soon as they are born. Adler found that females which were thus isolated, and which were shown by microscopic examination to be virgins, nevertheless laid eggs as soon as a caterpillar was furnished them.

Among 206 females which hatched from these eggs there were only 9 males, so that there is, in this species, a strong tendency for parthenogenetic eggs to produce females.

In the rose-gall-wasps Adler finds that the males are very rare, about one to fifty females, and he believes that they are superfluous, since the females in two species, *Rhodites rosæ* and *Rhodites eglanteriæ* are perfectly parthenogenetic, giving rise to parthenogenetic female offspring.

The instances of parthenogenesis in larval or immature insects are extremely interesting, but as they will be referred to at some length in another place I will not dwell upon them at present, as the cases which have been given are enough for our purpose, which is simply to show the satisfactory and exhaustive character of the proof that unfertilized eggs do in many animals develop and give rise to organisms which are in all respects like those born from fertilized eggs.

In *Nematus ventricosus* the males are not uncommon,

but Adler has verified Siebold's statement that in this species parthenogenesis of the ordinary females is not at all infrequent.

Although parthenogenesis is more frequent among the insects and crustacea than it is in other animals, it is not confined to these groups.

Cohn has given good reasons (*Zeit. f. Wiss. Zool.*, xii., 1863, p. 197) for believing that among the Rotifera the summer eggs, which give rise to both males and females, are parthenogenetic; while the winter eggs, which hatch into females exclusively, are the only ones which are fertilized. There is no reason for doubting the correctness of this conclusion, but it has not been placed beyond the possibility of all doubt, as is the case with so many insects.

Many observers have thought that they have found evidences of parthenogenesis in groups of animals where such an occurrence would be very exceptional, but in most of these cases there is much chance for error. Thus it has been stated that the eggs of echinoderms sometimes develop without impregnation, but when we recollect that both male and female echinoderms in most cases discharge their reproductive elements into the water, we can see that it must be almost impossible to state that the sea-water in which the eggs are placed contains no spermatozoa of the same species. Dr. J. M. Wilson has recently undertaken some experiments on this point at my suggestion. He fertilized a lot of eggs from one of our common sea-urchins, Strongylocentrotus, with male fluid from another of a distinct genus, Arbacia. A lot of Arbacia eggs were fertilized with a male Strongylocentrotus, a lot from each form with fluid from a male of the same species, and eggs from each species were placed in water without fertilization.

In all six cases the eggs gave rise to normal embryos; but that this was really due to the presence of spermatozoa in the water, was shown by the fact that no such surprising result followed in a second set of experiments where especial effort was made to get pure sea-water. Many of the recorded cases are open to the same objection; and in other cases, as in the virgin sou referred to by Bischoff, there seems to be some doubt whether the ova were really undergoing development; but Oelacher's observations on the eggs of a virgin hen ("Die Veränderungen des unbefruchteten Keimes des Hühnereies im Eileiter und bei Bebrütungsversuchen," *Zeit. f. Wiss. Zool.*, xxii., 1872, p. 220) seem to show that the hen's egg does have the power to pass through the first stages of development whether it is impregnated or not.

The instances of parthenogenesis which I have given show that this power may be independently acquired by animals which cannot possibly inherit it from a common source. In the vast majority of insects, and in the majority of the crustacea, the egg does not show the slightest tendency to develop before it is fertilized. It is true that in the case of the crustacea the evidence for this statement is almost entirely of a negative character, for no one has ever shown by experiment on any considerable number of species that the female cannot lay fertile eggs when the access of a male is prevented, but in many insects we know from actual observation that the eggs die soon after they are laid, unless they are fertilized; and we know enough of the breeding habits of crustacea to feel confident that parthenogenesis is exceptional among them, just as it is among insects.

We must, therefore, conclude that if we could retrace the course of evolution of any parthenogenetic animal we should be led back to an ancestral form which never

manifested any such power. It is impossible to believe that Daphnia and the honey-bee have inherited from a common parthenogenetic ancestor the power to produce fertile unimpregnated eggs, for the one form is much more closely related to normal insects and the other to normal crustacea than they are to each other. We may therefore state with confidence that the power has been independently acquired by many animals.

In the second place, we must admit that parthenogenetic ova are true ova in every sense: they are developed in an ovary like other eggs, and in many cases, as in those butterflies which are occasionally parthenogenetic, the very eggs which usually require impregnation may in rare instances develop without it. Weismann has made very careful examination as to the origin of both kinds of eggs in Leptodora, a water-flea related to Daphnia ("Ueber die Bildung von Wintereier bei Leptodora hyalina," *Zeit. f. Wiss. Zool.*, xxvii., 1876), and he finds that while there is some difference in the mode of origin of the winter eggs, which do not develop unless they are fertilized, and the summer eggs, which are parthenogenetic, the difference simply consists in the amount of nourishment which they receive in the ovary. In each case certain ova degenerate and are used up by the others as food, and a winter egg thus absorbs a greater number of these embryonic ova than a summer egg does; but Weismann's observations show that each of them is in all respects a true ovum, and that they are perfectly homologous with each other.

In some cases, as in some of the wasps described by Bassett and Adler, the animal which is born from a parthenogenetic egg differs considerably in structure from that which is born from a fertilized egg; but in other cases, as in butterflies and moths, there is no such

difference. In some cases, as in Daphnia, all the parthenogenetic eggs hatch into females ; in other cases, as in bees, they give rise to males alone; while in still other cases, as in the gall-wasps, some of the unfertilized eggs produce males and some females.

In many cases the animals which are thus produced are perfectly normal, and have nothing to distinguish them from those born from impregnated eggs. They have the ordinary structure of their species, and they are perfectly capable of propagating their kind. In some cases, as in the gallwasps, reproduction is preceded by the union of the sexes, and in other cases the animals born from parthenogenetic eggs are themselves parthenogenetic.

There is possibly one difference between ordinary and parthenogenetic eggs,—the presence of polar globules in the one case and their absence in the other; and I shall discuss this difference soon.

Except in this particular, the history of the development of the egg into the perfect animal is the same, whether the egg is fertilized or not. Weismann, who has studied the embryology of both parthenogenetic and fertilized eggs in insects ("Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insectenei"), shows that all the minuter details in the process of building up the embryo are the same, whether the egg is fertilized or not.

We must therefore believe that an ovum has in itself the power to give rise to a new organism, and that although it does not usually manifest this power, unless the egg is fertilized, it may exhibt it under certain circumstances, as parthenogenesis. Of the character of the circumstances which lead to parthenogenesis we know nothing, except that such circumstances have

thus acted in many groups of animals where the eggs ordinarily require to be fertilized.

Certain authors have suggested that there may be a connection between the extrusion of the "polar globules" from the ovum and the need of impregnation by a male cell.

The ripe ovarian ovum of an animal usually contains a transparent central body, the germinative vesicle, and when the egg is fully ripe the germinative vesicle approaches the surface and divides into two portions: one of these is discharged from the egg, thus forming the "polar globules." These take no part in the formation of the embryo. They become entirely separated from the egg, and soon die and disappear. The remainder of the germinative vesicle remains in the egg, as the "female pronucleus," which unites with the "male pronucleus" formed from the male cell after impregnation, and thus builds up a compound body, the first "segmentation nucleus."

The formation of these "polar globules" has been observed in all groups of the animal kingdom, except the rotifera and arthropods, and their functional significance is therefore a subject of the greatest interest. They obviously contain something which is not needed for the formation of the embryo, and they may be discharged from the egg before it is laid, or they may remain until it is laid, as seems to be the general rule, and may be discharged just before fertilization takes place, as is the case in the star-fish, or they may be discharged immediately after the egg is impregnated.

Within recent years an hypothesis regarding their significance has excited considerable notice. This hypothesis, which was first advanced by the late Prof. McCrady, and which is stated at length in Balfour's Treatise on

Comparative Embryology, is that each sexual element originally contains a male portion and a female portion; the ripe male cell is the male half of the male element, and the "polar globules" contain the male substance of the ovum, which is discharged in order that it may be replaced by the male element from the body of another organism. Balfour says: "I would suggest that in the formation of the polar cells part of the constituents of the germinal vesicle, which are requisite for its functions as a complete and independent nucleus, is removed to make room for the supply of the necessary parts to it again by the spermatic nucleus. My view amounts to the following, viz., that after the formation of the polar cells the remainder of the germinal vesicle within the ovum (the female pronucleus) is incapable of further development without the addition of the nuclear part of the male element (spermatozoon), and that if polar cells were not formed parthenogenesis might normally occur. A strong support for this hypothesis would be afforded were it to be definitely established that a polar body is not formed in the arthropoda and rotifera; since the normal occurrence of parthenogenesis is confined to these two groups in which polar bodies have not so far been satisfactorily observed. . . . To the suggestion already made with reference to the function of the polar cells, I will venture to add the further one, that the function of forming polar cells have been acquired by the ovum for the express purpose of preventing parthenogenesis. . . . There can be little doubt that the ovum is potentially capable of developing, by itself, into a fresh individual, and therefore, unless the absence of sexual differentiation was very injurious to the vigor of the progeny, parthenogenesis would most certainly be a very constant occurrence; and, on the

analogy of the arrangements in plants to prevent self-fertilization, we might expect to find some contrivance both in animals and plants to prevent the ovum developing by itself without fertilization. . . . On my hypothesis the possibility of parthenogenesis, or at any rate its frequency in arthropoda and rotifera, is possibly due to the absence of polar cells" (*Comp. Emb.*., vol. i. p. 63).

The simplicity of this hypothesis renders it very fascinating, but even if it were possible to accept it without qualification, it would not affect our argument, for it would still remain true that "the ovum is potentially capable of developing, by itself, into a fresh individual," and must therefore be very different in function from the male cell, which under no circumstances exhibits a similar power.

My reasons for doubting the hypothesis are, first, that a failure to discover polar cells in the eggs of rotifera or of the arthropods may be due to the fact that they are discharged very early in the history of the ovarian ovum. We know that in some animals, as in hydra, the polar cells are discharged while the egg is still contained in the ovary, and we also know that the eggs of many arthropods undergo in the ovary very peculiar changes, which greatly obscure their fundamental similarity to ordinary uncomplicated eggs, so that it is quite possible that our failure to discover the polar cells may be due to something else than to the fact that they are never formed. The eggs of insects especially are very peculiar, and Weismann says that "nirgends im ganzen Thierreich die Ontogenese so verschoben und coenogenetisch entartet ist" as it is among the insects. This author has figured, in the fertilized egg of a species of Chironomus, certain bodies which are not present in the

parthenogenetic eggs of Rhodites, and he suggests that these may be the long-sought polar cells, but he does not feel certain that this is the case, and examination of his paper will show that there is so much difference between the early stages of insect eggs and the corresponding stages of simpler and more typical eggs, that the identity of these bodies must remain open to some doubt.

There is another objection to the hypothesis, which seems to me to be entitled to great weight. According to Balfour's statement we should expect that any egg which retained the polar cells might develop without impregnation. Observers have failed to discover their extrusion in the eggs of ordinary arthropods, as well as in those which are parthenogenetic, and we should therefore expect all the arthropods to be parthenogenetic, but this is not the case. In many other animals, as in the oyster, they are not discharged until the egg is fertilized, and the hypothesis would require us to believe that an unfertilized oyster egg contains a male element as well as a female element; but when perfectly ripe oyster eggs are placed, without fertilization, under conditions which are perfectly favorable to development: they show no signs of life, and soon die and decay. If a little male fluid is added, however, they quickly discharge their polar cells, and then rapidly pass through the changes which build up the embryo.

If the polar cell is really equivalent to a male cell, we certainly might expect these oyster eggs, which are perfectly ripe, and, according to the hypothesis, contain all that is necessary for development, to show some power to develop without impregnation. If the power to extrude polar cells "*has been acquired by the ovum for the express purpose of preventing parthenogen-*

esis," we certainly should look for the occurrence of parthenogenesis in ripe ova which have not extruded these bodies.

However this may be, the correctness or incorrectness of the polar-cell hypothesis has no bearing upon our present argument, for the phenomena of parthenogenesis show beyond question that an egg may develop without union with a male cell, and there is no evidence whatever that a male cell ever acts in a similar way.

Other reasons for believing that the ovum and the male cell perform different functions in heredity.

Even if the possibility of parthenogenesis did not show us that the part played in heredity by the ovum is different from that played by the male cell, there are many other reasons for believing that the difference in the form of the two sexual elements corresponds to some profound difference of function.

I shall devote several chapters of this book to the extended discussion and proof of the facts which drive us to this conclusion, and I shall show that the belief in the essential similarity of the functions of the reproductive elements cannot possibly be retained.

When the male of one species or variety is crossed with the female of another species or variety, the hybrid offspring is often very different from that which is produced when the female of the first species is crossed with the male of the second. If the function of the ovum is the same as that of the male cell, we should have exactly the same elements in each case, and should expect the same result. The fact that the result is not the same proves that the elements are not the same either.

In many cases the male of one species will breed

freely with the female of the second species, while absolute sterility follows the union of a male of the second species with a female of the first species. The offspring of a male hybrid and the female of a pure species is much more variable than the offspring of a female hybrid and the male of a pure species. These facts are absolutely inexplicable, if the two sexual elements play similar parts in heredity.

A structure which is more developed or of more functional importance in the male parent than it is in the female parent is very much more apt to vary in the offspring than a part which is more developed or more important in the mother than it is in the father.

These facts, and many others which will be mentioned farther on, compel us to believe that there is some profound functional difference between the ovum and the male cell.

It is, therefore, only reasonable to distrust the absolute correctness and completeness of any hypothesis of heredity, which, like Darwin's Pangenesis hypothesis, recognizes no such difference.

Summary of last two Chapters.

The phenomena of heredity are certainly among the greatest marvels of the material universe, but there is no reason to believe that they lie outside the province of legitimate scientific inquiry. Our present purpose is not to trace them back to their origin or to show that they result from the properties of matter, but simply accepting them as vital phenomena, to trace the secondary laws to which their present form is due. The fact that the distinctive properties of the egg of any living species have been gradually acquired during the evolution of the race through the action of influences which

are, to a certain extent, open to observation and study, gives us ground for believing that we may hope to discover what it is in the structure of the egg, which renders these properties possible. There have been many attempts to do this, but it is impossible to accept any hypothesis which has ever been advanced. The evolution hypothesis, as advocated by Bonnet and Haller, is directly contradicted by the discoveries in the modern science of embryology, and it is accordingly now regarded as having only an historical interest, but the modern epigenesis hypothesis is no more satisfactory, for the resemblance between the evolution of a species from an unicellular ancestor and the development of an individual animal from an unicellular egg is only an analogy.

The efficient cause in the first case, the slow modification of the race by the natural selection of the most favorable variations, is absent in the second case, and there is nothing whatever to take its place. The parallelism between embryology, or the ontogenetic development of the individual, and phylogeny, or the evolution of the race, is one of the most remarkable and instructive generalizations of modern science, and the very existence of the parallelism gives us every reason to hope that an explanation of heredity or of ontogenetic development may be discovered: but to point out the parallelism is, in no sense whatever, to explain heredity.

If the conclusion be true which is accepted by most of the modern advocates of epigenesis, the conclusion that the egg which is to become a man differs in no essential particular from the egg which is to become a starfish, heredity is an insoluble mystery, for we neither possess nor have any grounds for believing that we ever shall possess any knowledge of forces competent to pro-

duce from two essentially similar eggs adult animals which are so essentially dissimilar. We cannot attribute this result to natural selection, for this law can only act on successive individuals; we cannot attribute it to the direct action of external conditions, for we know that eggs may give rise to very different animals when placed under identical surrounding conditions. Haeckel's statement that heredity is memory, contains a profound truth, as we have already seen, but it does not help us to understand heredity.

We know memory only in connection with organization, and if we believe that an egg contains the memory of all the past experience of the race, we must believe that it contains a complex organization to correspond to the complexity of this past experience.

So far as Haeckel's hypothesis of perigenesis has any claim to be considered an *explanation* of heredity, it is an hypothesis of evolution, not of epigenesis.

Jäger's view that the ovum is at first unspecialized, and that it gradually assimilates from its developing parent all the specializations of the structure of the latter, fails to account for reversion or for the transmission of adult characters by immature parents, and the author is compelled to substitute for it an evolution hypothesis when he comes to treat of reversion.

There is no escape from the conclusion that the ovum of an animal actually contains in some form the potentiality of that particular animal, and Huxley acknowledges that the development of an egg is in essence a process of evolution.

We thus find ourselves driven back from the modern hypothesis of epigenesis to the long abandoned hypothesis of evolution, and we must therefore inquire whether our recent great advances in knowledge of the forces

which have produced the various forms of animal and vegetable life, will guide us nearer to the truth than the speculations of the last century. Bonnet and Haller might fairly assume that each species had been what it is now "from the beginning," but we cannot nowaday make any such assumption, and we must believe that the structure of the germ, like the structure of the adult animal, has been gradually acquired by natural selection.

A modern hypothesis of evolution must therefore be a very different thing from the one which Bonnet furnished, and must account for the slow advancement of the germ from generation to generation.

In Darwin's pangenesis hypothesis we have a provisional explanation based upon the generalizations of modern science. It is a true evolution hypothesis, for Darwin believes that an ovum or a male cell is a wonderfully complex structure, and that it contains gemmules to represent each feature in the organization of the adult. One essential difference between this hypothesis and the original hypothesis of evolution as stated by Bonnet, is that Darwin believes that the ovum contains, not the perfect animal in miniature, but a distinct germ for each distinct cell or structural element of the adult. Darwin's hypothesis recognizes the gradual specialization of the ovum during the evolution of the race, for each cell of the body of the parent may at any time transmit to it new gemmules. Most of the objections to it are based upon its complexity, and on the almost infinite number of gemmules which it requires; but besides these objections we know from Galton's experiments that it is impossible to accept it without modification. We also have, in the fact that the functions of the two sexual elements are not alike, a reason for believing that,

although it may be an approximation to the truth, it cannot be regarded as a complete and satisfactory explanation.

The object of this work is to present a new hypothesis which will be seen to bear a close resemblance to the one which has been advocated by Darwin, although careful examination will show that it is in reality very different. I hope to show that it is not open to the objections which are urged against the pangenesis hypothesis, while it contains all the features which give value to the latter.

CHPTER IV.

A NEW THEORY OF HEREDITY.

The objection to the hypothesis of pangenesis would be almost entirely removed if it could be simplified—Statement of a new theory—Heredity is due to the properties of the egg—Each new character has been impressed upon the egg by the transmission of gemmules—Tendency to form gemmules is due to the direct action of external conditions—The ovum is the conservative element—The male cell is the progressive element—This theory has features of resemblance to most of the hypotheses which have been noticed—It fills most of Mivart's conditions also—It is not necessary to assume that the ovum is as complicated as the adult—There are many race characters which are not congenital—There are many congenital characters which are not hereditary—Direct action of external conditions—Our theory stands midway between Darwin's theory of natural selection and Lamarckianism.

If the hypothesis of pangenesis could be so remodelled as to demand the transmission of only a few gemmules from the various parts of the body to the reproductive elements, instead of the countless numbers which are demanded by the hypothesis in its original form, we should escape many of the objections which have been urged against it.

If it can be shown that these few gemmules are not necessarily present at all times and in all parts of the body, but only occasionally and in certain regions, we shall escape the difficulty presented by Galton's experiments, and the presumption in favor of the hypothesis will be greatly increased.

If the theory of heredity, in its new form, agrees with

all that we know of the functions of the two sexual elements and if, besides furnishing an explanation of all the phenomena which are accounted for by other hypotheses, it embraces new classes of facts as well, the presumption in its favor becomes still greater.

Finally, if it leads to the discovery of new and unexpected relations between phenomena, and to the establishment of laws which group and interpret phenomena between which no connection had previously been recognized, its value must be acknowledged.

I venture, then, to advance a new theory of heredity, which, briefly stated, is as follows:

The union of two sexual elements gives variability. Conjugation is the primitive form of sexual reproduction. Here the functions of the two elements are alike, and the union of parts derived from the bodies of two parents simply insures variability in the offspring.

In all multicellular organisms the ovum and the male cell have gradually become specialized in different directions.

The ovum is a cell which has gradually acquired a complicated organization, and which contains material particles of some kind to correspond to each of the hereditary characteristics of the species.

The ovum, like other cells, is able to reproduce its like, and it not only gives rise during its development to the divergent cells of the organism, but also to cells like itself.

The ovarian ova of the offspring are these latter cells, or their direct unmodified descendants.

Each cell of the body is, in a morphological sense, an independent individual. It has the power to grow, to give rise by division to similar cells, and to throw off minute germs. During the evolution of the species it has

by natural selection acquired distinctive properties or functions, which are adapted to the conditions under which it is placed. So long as these conditions remain unchanged it performs its proper function as a part of the body; but when, through a change in its environment, its function is disturbed and its conditions of life become unfavorable, it throws off small particles which are the germs or "gemmules" of this particular cell.

These germs may be carried to all parts of the body. They may penetrate to an ovarian ovum or to a bud, but the male cell has gradually acquired, as its especial and distinctive function, a peculiar power to gather and store up germs.

When the ovum is fertilized each germ or "gemmule" unites with, conjugates with, or impregnates, that particle of the ovum which is destined to give rise in the offspring to the cell which corresponds to the one which produced the germ or gemmule; or else it unites with a closely related particle, destined to give rise to a closely related cell.

When this cell becomes developed in the body of the offspring it will be a hybrid, and it will therefore tend to vary.

As the ovarian ova of the offspring share by direct inheritance all the properties of the fertilized ovum, the organisms to which they ultimately give rise will tend to vary in the same way.

A cell which has thus varied will continue to throw off gemmules, and thus to transmit variability to the corresponding part in the bodies of successive generations of descendants until a favorable variation is seized upon by natural selection.

As the ovum which produced the organism thus selected will transmit the same variation to its ovarian

ova by direct inheritance, the characteristic will be established as an hereditary race characteristic, and will be perpetuated and transmitted, by the selected individuals and their descendants, without gemmules.

According to this view, the origin of a new variation is neither purely fortuitous nor due to the direct and definite modifying influence of changed conditions. A change in the environment of a cell causes it to throw off gemmules, and thus to transmit to descendants a tendency to vary in the part which is affected by the change.

The occurrence of a variation is due to the direct action of external conditions, but its precise character is not. My view of the cause of variation is thus seen to be midway between that accepted by Darwin and that advocated by Semper and other Lamarkians.

Many naturalists have given reasons for believing that the transmutation of species is not always gradual, but that a form which has long persisted without change may suddenly vary greatly, and thus give rise to a strongly-marked race of descendants. Mivart has discussed this subject at considerable length, and he quotes Professor Huxley's opinion that "we greatly suspect that Nature does make considerable jumps in the way of variation now and then, and that these saltations give rise to some of the gaps which appear to exist in the series of known forms;" and Dall has proposed the term *saltatory evolution* for abrupt change of this kind. According to the theory here advanced, variation must tend to accumulate or culminate, and one variation must cause others; for when any particular cell changes, the harmonious adjustment between it and adjacent or related cells will be disturbed, and all the cells which are thus affected will tend to throw off gemmules, and thus to induce variability in the same cells of succeeding generations. Then, too, a

gemmule may unite or conjugate in the ovum with particles which are not perfectly equivalent to it, but only very closely related to it. Thus a variation may affect a considerable number of related cells at the same time, or a variation in any part may cause in succeeding generations the variation of homologous parts, thus producing what Darwin has called *correlated variation.* We can also understand how it is that when any part of a complicated organ varies, variations in other parts of it are also soon presented for the action of natural selection, so that an harmonious readjustment is soon established.

According to this view we must believe that all the characteristics which are established as true race-characteristics, as hereditary peculiarities of the species, are transmitted by the ovum, which has in itself the power to develop, when excited by a proper stimulus which may or may not be due to impregnation, into a new individual of the parent form.

New variations, on the other hand, are produced through the agency of gemmules thrown off from cells like those in which the variation appears.

Gemmules may penetrate to all parts of the body, and they may thus give rise to bud-variation and to analogous changes; or they may penetrate to an ovarian ovum and give rise to variation without fertilization: but as these phenomena depend upon chance, they are comparatively rare, while the aggregation of the gemmules in the male cell and their transmission by impregnation are normal processes.

According to this view, the male element is the originating and the female the perpetuating factor; the ovum is conservative; the male cell progressive. Heredity or adherence to type is brought about by the ovum;

variation and adaptation through the male element; and the ovum is the essential, the male cell the secondary, factor in heredity.

The various hypotheses which we have noticed have little in common, and it is therefore interesting to note that they all present points of resemblance to the one which is here advanced, and that this alone has features in common with them all.

Like Aristotle and the ancients, we must believe that the two reproductive elements play widely different parts. Like Bonnet and Haller, we see that the structure of the adult is latent in the egg.

The mode of origin and transmission of the gemmules is essentially like Darwin's conception, and we must acknowledge that Buffon's view of the part played by his organic molecules was very near the truth.

The analogy upon which Haeckel lays so much stress is readily explicable by our theory, for since each stage in the evolution of the species has been impressed by gemmules upon the egg, it is, in truth, *only natural* that the developing organism should mirror the ancestral history of its species; and, finally, our view of the origin of the properties of the ovarian egg is identical with that given by Jäger in his explanation of reversion.

An honest attempt to reason from the phenomena of nature can hardly fail to result in the discovery of some little truth, and I think we may hope that all these points of agreement with hypotheses which are manifestly inadequate can only be due to the presence in them all of some portion of the true light of nature.

Mivart, who believes with Darwin that natural selection has been a great but not the exclusive means through which organisms have been modified, has attempted in Chapter xi. of his book on the *Genesis of Species* to

indicate some of the requisites of a true theory of the origin of species. This valuable and instructive book is well worthy of careful study, and most students will find in it much material for reflection. Mivart has no explanation of his own to offer, and some of the characteristics of the explanation which he believes in, but does not furnish, are conspicuously absent in the present attempt as well as in Darwin's work; but it is interesting to note that many of the conditions which he enumerates are complied with by our theory of heredity, and by no other explanation which has ever been proposed. Thus he says (p. 244) that "It is quite conceivable that the material organic world may be so constituted that the simultaneous action upon it of all known forces, mechanical, physical, chemical, magnetic, terrestrial and cosmical, together with other as yet unknown forces which probably exist, may result in changes which are harmonious and symmetrical, just as the internal nature of vibrating plates causes particles of sand scattered over them to assume definite and symmetrical figures when made to oscillate in different ways by the bow of a violin being drawn along their edges. The results of these combined internal powers and external influences might be represented under the symbol of complex series of vibrations (analogous to those of sound and light) forming a most complex harmony or a display of most varied colors.

"In such a way the reperation of local injuries might be symbolized as a filling up and completion of an interrupted rhythm. Thus also monstrous aberrations from typical structure might correspond to a discord, and sterility from crossing be compared with the darkness resulting from the interference of waves of light.

"Such symbolism will harmonize with the peculiar

reproduction, before mentioned, of heads in the body of certain annelids, with the facts of serial homology, as well as those of bilateral and vertical symmetry. Also as the atoms of a resonant body may be made to give out sound by the juxtaposition of a vibrating tuning-fork, *so it is conceivable that the physiological units of a living organism may be so influenced by surrounding conditions (organic and other) that the accumulation of these conditions may upset the previous rhythm of such units, producing modifications in them—a fresh chord in the harmony of Nature—a new species.* . . . It seems probable, therefore, that new species may arise from some constitutional affection of parental forms—an affection mainly if not exclusively of their generative system."

According to the view which I have presented a new variation is caused in essentially the manner which Mivart suggests as probable. The accumulated influence of surrounding conditions, organic and inorganic, does upset the previous rhythm of the physiological units of the living organism, and causes them to give rise to gemmules, and the tendency of the corresponding units of the offspring to vary, is directly due to this constitutional affection of the parental forms.

I have spoken of the egg as containing material particles of some kind to represent each of the hereditary congenital peculiarities of the race. According to this view the egg of one of the higher animals must be a wonderfully complex structure. At first sight it would seem as if it must be as complicated as the adult animal, but a little thought will show that this is by no means the case.

In the first place, there are many structures which enter into the formation of the body without being part of its actual living substance. Nearly every living

body consists in part of structures which are in no sense alive, but which are built up by the formative activity of the living protoplasm. The shell of a snail or of an oyster is purely inorganic, and although it is built up by the animal, and is necessary to its existence, it is no more a part of the living substance of the animal than the shell which is picked up and inhabited by a hermit crab. It is true that the oyster's shell is formed by the animal, as part of itself, but the shell does not grow, like living tissues, by the absorption and transformation of nutriment, but by the crystallization of the amorphous mineral matter which is poured out by the living cells of the mantle; and microscopic examination shows that it is not an organized tissue made up of cells, but an aggregate of purely mineral crystals.

Since this is the case it is clear that it is not the shell itself, but a tendency to build the shell, which is hereditary, and is contained in the egg; and an illustration will serve to show that the inheritance of the tendency involves much less complexity in the structure of the egg than the inheritance of the thing itself would imply.

A bee inherits a tendency to build up a comb of wax, and to fill the cells of this comb with honey.

The comb and the honey are due to the vital activity of the bee, just as the shell is the result of the vital activity of the oyster; but the statement that the bee's egg contains something which corresponds to the structural organization to which the tendency is due, is certrinly not equivalent to a statement that the actual comb, filled with honey, is represented in the egg. This is just as true of structures which are built up, inside the body, by its vital activity, as it is of those which are built up in the same way outside the body.

When we take into account all structures of this kind

which are not parts of the living substance of the organism, but which simply owe their existence to the properties of its living substance, we can readily understand that the complexity of an adult animal may be vastly greater than the complexity of the egg.

In the second place we must recollect that there are many race characteristics which are of constant occurrence without being hereditary.

Organisms are often greatly modified by the direct action of external conditions; for instance, a tree may be dwarfed by insufficient food, or the muscles of a limb may be greatly enlarged by unusual work. If all the individuals of a species are similarly exposed to conditions of this sort, they will all be acted upon in the same way, and the modification which is thus produced will be characteristic of the species, without being hereditary.

To take one of the simplest cases: Trees which grow upon mountain-tops, where they are exposed to extreme changes of climate, and to constant and violent winds, have a very characteristic appearance, which is familiar to all mountain climbers. In some cases this peculiar form is hereditary, and persists in seedlings which are grown in more favored regions, but in other species the transplanted trees show, by losing their peculiarities, that these are due to direct modification.

If a certain species occurs naturally nowhere except in such situations, this species will be characterized by its dwarfed size and by its twisted and distorted branches; but if individuals reared under favorable influences grow and flourish and become regular and symmetrical, we may conclude that the characteristics of each wild individual are caused by its scanty food and constant exposure, and that they are not represented in the egg, and are not congenital.

If this experiment is impossible, if all the transplanted trees die, and if the seeds fail to germinate in fertile ground, there will be no way to show whether the peculiar characteristics of the species are or are not hereditary.

We know that organisms may be modified in many ways by the direct action of external conditions, but a few illustrations will not be out of place.

Hemp-seed causes bullfinches and certain other birds to become black, and we know from the observations of many naturalists that caterpillars which are fed on different kinds of food either themselves acquire a different color, or they may produce moths which differ in color. Many curious cases of this kind have been noticed in birds and insects, and if unnatural food causes deviations from the natural color of a species, it is quite possible that the normal color may in many cases be due directly to the action of the normal or natural food.

Darwin gives many instances of plants which are characterized by a certain peculiarity in one country, while in another country this peculiarity is almost or entirely lacking. Thus when the American sassafras tree is grown in Europe, it loses its aromatic flavor. In India the fibres of flax and hemp are brittle and useless, and the latter plant yields a resinous narcotic substance, hasheesh, which is used as an intoxicating drug, but in England this property is lost and the fibre becomes long and tough. Large, finely-flavored, and brightly-colored American apples, when reared in England, produce fruit of a dull color and poor quality.

In these cases we are unable to state what the determining conditions are, but the fact that peculiarities are made to disappear by a change from one country to another shows that they are not congenital but are due

to something outside the plant, which is present in one country but absent in another. The following instance, which is given by Darwin, is most interesting: "Mr. Salter, who is well known for his success in cultivating variegated plants, informs me that rows of strawberries were planted in his garden in 1859, in the usual way; and at various distances in one row several plants simultaneously became variegated, and what made the case more extraordinary, all were variegated in precisely the same manner. These plants were removed, but during the three succeeding years other plants in the same row became variegated, and in no instance were the plants in any adjoining row affected." He also says that in certain parts of India the turkey becomes reduced in size with the pendulous appendages over the head enormously developed.

In these cases it is difficult to determine what has caused the change, but in other instances this is more obvious. Thus Darwin states that good authorities assert that horses kept during several years in the deep coal mines of Belgium become covered with velvety hair almost like that of the mule, and he quotes from Dr. Falconer the statement that the Thibet mastiff and goat when brought down from the Himalayas to Kashmir lose their fine wool.

These are only a few of the cases which Darwin gives, and many more might be added from other authorities, but I have given enough to show that external conditions of life may act in one country to cause certain modifications which are entirely absent in another country.

The change of Artemia into Branchippus, by rearing it in fresh water, is one of the most remarkable instances of definite modification due to a change of external

conditions. Artemia salina is a small crustacean, found in the salt lakes of America, Europe, and Africa. When this species is kept in water in which the quantity of salt is gradually diminished, it becomes transformed, in a few generations, into what has been described as a distinct species—Artemia Milhausenii—and if the process of diluting with fresh water is continued until it finally becomes perfectly fresh, the Artemia becomes changed into the well-known fresh-water form Branchippus, which has always been considered a distinct genus.

Semper has shown (*Animal Life*, p. 161) that certain definite changes in the size of the fresh-water snail Lymnæa are produced in a short time by confining it in a small quantity of water.

These are a few of the cases where we are able to show, by experiment, that certain race-characteristics are not congenital, but are due to external influences, and we have every reason to believe that the same thing is true in many cases which have never been made the subject of experiment, and in many more where experiment is impossible, since the change would cause death rather than modification.

The possibility that structures of the greatest constancy and importance may not really be hereditary is well illustrated by Hunter's well-known experiments on the sea-gull. In pigeons, and in most birds which feed upon grain, the muscular wall of a portion of the stomach is greatly developed, to form the crushing and grinding gizzard, which is lined with a covering of tough membrane, while the stomach of the gull and of most flesh-feeding birds is soft, and the muscular layer little developed. Hunter fed a sea-gull for a year on grain, and he thus succeeded in hardening the inner coat of the bird's stomach, thus forming a true gizzard; and Dar-

win quotes from Dr. Edmonston the statement that a similar change occurs twice a year in the stomach of another sea-gull in the Shetland Islands, where this bird frequents the corn-fields and feeds on seeds in the spring, but catches fish during the rest of the year. This observer has noticed a great change in the stomach of a wren which had long been fed on vegetable food; and Menetries states that when an owl was similarly treated the form of the stomach was changed, and the inner coat became leathery, while the liver increased in size. Semper states that Dr. Holmgrin has been able to transform the gizzard of a pigeon into a carnivorous stomach by feeding the bird on meat for a long time.

There is no reason for believing that the few cases known to us are all which are due to the direct action of external conditions, and we must acknowledge that there may possibly be many structural characteristics of animals and plants which are not hereditary, but are constant simply because the conditions which cause them are constant, and as we are only compelled to attribute to the ovum representatives of all the hereditary race characteristics, it will be seen that the structural complexity of the egg may be vastly less than that of the developed organism.

This is not all, however. There may be many congenital race characteristics which are not hereditary.

The various parts of a developing organism are exposed in countless ways to the influence of other parts. The simplest illustration of this fact is the mechanical pressure exerted upon each other by the developing viscera.

This is a subject which is almost outside the province of experiment, for we cannot shut out the influence of any particular organ without removing the organ itself, and the removal of any organ of considerable size is

more likely to cause death than to cause modification. The features of microcophalous idiots show us, however, that the shape of the skull and of the face is only due, in part, to heredity, and is, in part at least, due to the size and shape of the brain. In lop-eared rabbits the whole conformation of the skull is altered by the mechanical pressure of the drooping ears, and it is stated that certain monstrosities in the shape of snail-shells are due to the arrested development of the reproductive organs. Moquin-Tanden remarks that with plants the axis cannot become monstrous without in some way affecting the organs subsequently produced from it.

We can see, from the study of domesticated pigeons, that an increase or a decrease in certain organs is a direct cause of modification in other parts. Pouter pigeons have been selected for length of body, and the establishment of a long-bodied race has increased the number of their vertebræ and the breadth of their ribs. Tumblers have been selected for their small size, and the number of ribs and of primary wing-feathers has thus been reduced. Fantails have been selected for their large widely-expanded tails, with numerous tail-feathers, and the size and number of the caudal vertebræ have thus been increased, and the selection of long-beaked carriers has increased the length of their tongues. Cline states that the skull of a ram with horns weighs four times as much as that of a hornless ram of the same age, and Youatt states that in hornless cattle the frontal bones are materially diminished in breadth towards the poll, and the cavities between the bony plates are not so deep, nor do they extend beyond the frontals.

The kidneys of different birds differ much in size, and St. Ange believes that this is determined by the size of the pelvis.

It is plain that if the character of important parts can be thus changed by changes in other parts, the typical or characteristic form of these parts may be due only partially to heredity.

We see then that the structural complexity of an adult animal is due in part to the formation of structures which are not alive, in part to the direct modifying influence of external conditions of life, and in part to the action of one organ of the body upon another, so that the number of features which are directly inherited is very much less than the number which are constant in and characteristic of the species.

It is impossible for us to state at present how many features must be subtracted from the race characteristics of an animal in order to give us the total number of hereditary congenital characteristics. The observations and experiments which are recorded are few in number, but they are sufficient to show us that, in all the higher animals, very considerable deduction must be made, and we may be sure that the mature animal is vastly more complex than the egg. There is still another limiting circumstance which has not yet been mentioned.

Many of the parts of an organism are due to indefinite multiplication of a single element. The simplest illustrations of this fact are the blood corpuscles of vertebrates and the leaves of plants. It is clearly unnecessary to suppose that each vertetrate ovum contains separate particles for all the blood corpuscles, or that each seed contains separate particles for all the leaves which the plant is to produce. All that is necessary is to assume that it contains particles which are capable of producing a single one of these structures, with a capacity for indefinite multiplication, and that surrounding conditions determine how far, and in what places,

this power of multiplication shall manifest itself. Most of the organs of the body contain great numbers of cells which are alike both in structure and function, and as it is usually quite impossible to say how far the size of an organ is truly hereditary, and how far it is determined by surrounding conditions, it is, of course, impossible to say to what extent its mature structure is represented in the ovum, but as we know that the size of most organs varies, and may be increased or diminished by external influences, we may be quite certain that the number of independent cells which make up the tissues and organs of a mature organism, is very much greater than the number represented by distinct particles in the ovum.

It is not even necessary to suppose that all classes of cells which are present in the adult are represented in the ovum. In a mammal, for instance, certain epithelial cells become converted into hairs, while others become converted into glands or other specialized epithelial structures.

It is not necessary to assume that all of these specializations are represented in the ovum, for we know that ordinary epithelial cells, in a part of the body where no hair is normally developed, may, when inflamed, give rise to hairs. It is therefore quite possible that each epithelial cell may, when excited by the proper influence, tend to become converted into a hair cell. Each cell of the body may possess the tendency to manifest certain properties under certain conditions, and to manifest certain other properties under other conditions, and the descendants of a single cell may thus become modified in several divergent directions, and each modification may be perfectly constant and characteristic of the race without being hereditary; that is, without being represented in the ovum by a particle with the same specialization.

It may seem to some that the assumption that the egg contains particles capable of producing an unspecialized epithelial cell which shall have the power to give rise to all the specialized sorts of epithelial cells, involves just as much complexity of structure as the assumption that each kind of cell is represented in the ovum, but I think an illustration will show that this is not the case.

Training of a certain kind will develop a boy into a good pedestrian, while another sort of training will make him a good shoemaker; but it is surely simpler to assume that he is born with a tendency to develop the characteristics of a shoemaker under the influence of certain conditions, and those of a pedestrian under other conditions, than to assume that he is born with all the peculiarities of both latent in his organization.

The direct modifying influence of surrounding conditions is a subject upon which very much remains to be done, but we know enough about it already to state that many of the constant characteristics of organisms are due to exposure to constant and uniform conditions rather than to heredity. To what extent this is true we are quite unable to determine, but we can be sure that the organization of the ovum is simpler, and in all probability vastly simpler, than that of the developed organism.

After all these deductions are made the number of strictly hereditary features is very great indeed, and the egg of one of the higher animals must be a marvellous structure, for we know that, after all, most of the characteristics of an organism are not due to the influence of its conditions of life, but to the past history of the race; and Darwin has shown us that the successive changes which have resulted in the evolution of any organism do not, usually, owe their existence to the direct modify-

ing effect of external influences, but to the natural selection of congenital variations.

The fact that our theory requires us to believe that the egg of one of the higher animals is complex beyond our powers of conception, must not be regarded as an argument against the theory, for we are compelled to believe this in any case. The difference between our theory and other attempts to explain the phenomena of heredity, is that it does what no other hypothesis attempts. It furnishes a simple explanation of the manner in which the ovum has acquired its present complexity.

In the following chapters I shall give some of the reasons for believing that the difference between the functions of the sexual elements which the theory requires does actually exist, but even in the absence of this proof it would be natural to conclude that if race modification could be furthered and aided by the divergent specialization of the functions of the two reproductive elements, natural selection would, in all probability, have acted so as to bring such a specialization about.

We know that the influence of natural selection is constantly exerted to seize upon and perpetuate any tendency to division of labor among the organs and tissues and cells of the body, and it is only natural that the successive stages in the specialization of the sexual elements should have been perpetuated like any other useful specialization.

CHAPTER V.

ON THE OPINION THAT EACH SEX MAY TRANSMIT ANY CHARACTERISTIC WHATEVER.

The argument from hybrids—This argument is inconclusive—The argument from the homology between the ovum and the male cell—Homology does not involve functional similarity—The argument from the dual personality of each individual; from reversion; and from polymorphism—These phenomena admit of a simpler explanation—Summary of chapter.

The Argument from Hybrids.

According to the view to be presented in this work, the functions of the two sexual elements, in inheritance, are not alike.

The proof of this will be presented further on, when the subject is reached in the logical course of the development of our argument.

Some of the very highest authorities have been led to a view which is directly opposite, and have held that either parent may transmit to the offspring any characteristic whatever. Lest any reader should assume, at the beginning of this book, that the work involves an absurdity, and that my conclusion is already disproved, it seems best to at once examine the reasons for the opposite view. If I can show that these reasons are inconclusive, and that there is and can be no proof for the statement that each sexual element transmits to the offspring every characteristic of the parent, we can then enter into the subject without prejudice, and can wait

for the proper time to present the proof of the opposite view, that the two sexual elements play different parts in heredity.

If the authority of great names counted for anything whatever in science, the case against me would be very strong, but where an appeal to nature is possible, authority counts for nothing.

Darwin's place among the students of heredity is certainly the highest, and he takes very strong ground indeed upon this subject.

Thus he says (*Variation of Animals and Plants,* Vol. ii. p. 88): "I am aware that such cases (of prepotency) have been ascribed by various authors to such rules as that the father influences the external characters, and the mother the internal characters.

"But the great diversity of the rules given by various authors almost proves their falseness. Dr. Prosper Lucas has fully discussed this point, and has shown that none of the rules (and I could add others to those quoted by him) apply to all animals. Similar rules have been announced for plants and have been proved by Gärtner to be all erroneous."

In the *Anatomy of Invertebrated Animals,* p. 30, Huxley states that "no structural modification is so slight, and no functional peculiarity is so insignificant *in either parent,* that it may not make its appearance in the offspring."

Darwin, in many parts of his writings, is still more explicit. Thus he says (*Variation of Animals and Plants,* Vol. ii. p. 431): "Ovules and the male element, before they become united, have, like buds, an independent existence. *Both have* the power of transmitting *every single character* possessed by the parent form. We see this clearly when hybrids are paired *inter se,* for

the characters of either grandparent often reappear, either perfectly or by segments, in the progeny. *It is an error to suppose that the male transmits certain characters and the female other characters.*"

I think a little examination will show clearly the impossibility of proving this statement from the phenomena of crossing. In order to breed together animals must be closely related; they must belong to the same species or to two closely allied species. Since the individuals which belong to two closely related species are the descendants of a common, and not very remote, ancestral species, it is clear that almost the whole course of their evolution has been shared by them in common; all their generic characteristics being inherited from this ancestor. Only the slight differences in minor points, which distinguish one species of a genus from another, have been acquired since the two diverged, and not even all of these slight differences, for a difference between two allied species may be due to the fact that while one has been modified the other has retained, unmodified, certain resemblances to their common ancestor. We know that the duration of even the most persistent species is only an infinitesimal part of the whole history of their evolution, and it is clear that the common characteristics of two allied species must outnumber, thousands of times, the differences between them. It follows that the parents of any possible hybrid must be alike in thousands of features for one in which they differ. It is therefore out of the question to attempt to prove, from the phenomena of crossing, that each parent can transmit to the child all its characteristics. Crossing simply results in the formation of a germ by the union of a male and a female element derived from two essentially similar parents, with at most only a few secondary

and comparatively slight differences, all of which have been recently acquired.

If a perfect animal could be developed from the spermatozoon of a male parent, as it can be, in cases of parthenogenesis, from the ovum of a female parent, we should have a means of proving that each sex transmits its entire organization to its offspring.

The phenomena of parthenogenesis prove that the female does actually thus transmit its entire organization, but there is nothing to show that the male parent does also, for it is clear that, from the nature of the case, the phenomena of crossing are incompetent to prove it.

The Argument from the Homology of the Male and Female Sexual Elements.

Many authors have gone much further than the statement that any characteristic whatever may be transmitted by either parent, and have held that the offspring is actually a dual personality, made up of a complete organization or individuality inherited from the father, and another, equally complete, inherited from the mother. This view has found favor with a number of modern writers, and frequently makes its appearance in the literature of the subject.

Thus Huxley says (*Encyclop. Brit., Art. Evolution*), "It is conceivable, and indeed *probable,* that every part of the adult contains molecules derived from the male and from the female parent; and that, regarded as a mass of molecules, the entire organism may be compared to a web, of which the warp is derived from the female, and the woof from the male. And each of these may constitute an individuality in the same sense as the whole organism is one individual, although the matter of the organism has been continually changing."

It will be found, on examination, that there is much to be said in support of this view, although I believe that there is a much simpler explanation of the facts which seem to favor it.

The only reason given by Huxley, in the article above quoted, is the homology between the ovum and the spermatozon; the fact that in all the higher animals and plants the germ is formed by the union of one nucleated cell, the ovum, with another more or less modified nucleated cell, the male cell, and that the structural components of the body of the embryo are all derived, by a process of division, from the coalesced male and female germs.

In answer to this we may point out that while the hypothesis requires that a wasp born from a fertilized egg should differ essentially from one born from a parthenogenetic egg, the one being a dual person and the other a unit, we do not find any obvious difference corresponding to the supposed molecular difference. We should not expect a wasp with a dual personality to be, to all appearances, exactly like one with a single personality.

A fatal objection to Huxley's argument, above given, is that, at bottom, it is simply an assumption that the homology or morphological equivalence of the ovum and male cell proves their functional equivalence. The fallacy of this assumption hardly needs notice, since it is well known that homology is no evidence whatever of functional resemblance. The quill feathers which fit a bird's wing for flight are homologous with the scales which cover and protect the arms and fingers of a crocodile, but we could hardly name two structures which serve more different purposes. The homology between them simply indicates that, at some time in their his-

tory, both scales and feathers have had a common origin in an epidermic structure, which has gradually become specialized into these organs.

While the homology between the ovum and the male cell is no reason for assuming that their functions are now alike, the constant differences between them, throughout almost all of the organic world, seem to afford a very convincing reason for believing that their functions have been specialized in two divergent directions.

If we can show that good might have resulted to the organism from such specialization, and from the restriction of certain parts of the reproductive function to one element, and the restriction of others to the other, we may feel confident that, provided variations in these directions have at any time arisen, natural selection would have seized upon and perpetuated them.

I hope to show the great usefulness of a specialization of this sort, and if I can do so, it is clear that the known differences between the ovum and the spermatozoon are reasons for a belief in its existence, while the only conclusion which can be drawn from the homology between them is, that at one time their functions were alike.

The Arguments from the Transmission of Latent Sexual Characteristics; from Reversion, and from Alternation of Generations.

In addition to the reason given by Huxley for a belief in the dual nature of each organism, he might have adduced the fact that the characteristics of each sex are potential and latent in the organism of the opposite sex, as is proved by the transmission by a father to his daughter of characteristics inherited from his grandmother.

The fact that the characteristics of one sex are latent

in the organism of the other is proved by countless well-known illustrations, and it seems, at first sight, to afford evidence of the dual personality of each animal.

The fact in itself is so interesting that, while I believe in the possibility of a much simpler and more satisfactory explanation, it will not be out of place to devote a little space to the subject.

"In every female all the secondary male characters, and in every male all the secondary female characters, apparently exist in a latent state, ready to be evolved under certain conditions" (Darwin, *Variation. Vol.* ii. p. 68).

A perfect beard often begins to grow upon the face of a woman after the power of reproduction is lost by age or disease. Such women are often alluded to by Roman authors under the name of "viragines," and Hippocratus (*De Morb. Vulg., Lib.* vi. 55–56) has left us the description of two well-marked instances.

Aristotle (*Hist. Animal,* ix. cap. 36) gives an account of a hen which had ceased laying, and assumed the characteristics of the male bird, and similar change in female birds has been recorded by many writers. It has been observed in the hen, common pheasant, golden pheasant, silver pheasant, turkey, pea-hen, partridge, bustard, pelican, various ducks, cuckoo, cotinga, chaffinch, bunting, and other birds. The change may be produced by age, by disease of the ovaries, removal of the ovaries, and even (*Yarrel, Phil. Trans.* 1827, ii. p. 268) by removal of part of the oviduct.

Old hens which have stopped laying often acquire a comb, wattles, spurs, the brightly-colored plumage and long tail-feathers of the cock, assume the habits of the male, and even learn to crow. The bad character, as layers, of crowing hens, has even given rise to a proverb.

According to Darwin, Waterton gives a curious case of a hen which had ceased laying, and had assumed the plumage, voice, spurs and warlike disposition of the cock: when opposed to an enemy she would erect her hackels and show fight.

Female deer often acquire the horns, peculiar hair, ears, odor, and sexual desire of the males.

On the other hand, it is well known that the secondary sexual characteristics of male animals are more or less completely lost when they are subjected to castration.

Darwin states, on the authority of Yarrell, that if the operation be performed on a young cock, he never crows again; the comb, wattles and spurs do not grow to their full size, and the hackels assume an intermediate appearance between the true hackels and the feathers of the hen. Similar results are said to be produced by confinement.

Buffon states (*Hist. Nat., Tom.* vi. p. 80) that the horns of a stag castrated during the rutting season become permanent, but that new horns do not usually appear if it is castrated when out of heat.

Simpson says (*Cyc. of Anat., Vol.* ii. p. 717), "From the frequency with which castration is performed, the effect of the testes in evolving the general sexual peculiarities of the male have been more accurately ascertained than that of the ovaries upon the female constitution. These effects vary according to the age at which the removal takes place. When an animal is castrated some time before it reaches the term of puberty, the distinctive characteristics of the male are in general never developed; and the total absence of these characters, together with the softness of their tissues, the contour of their form, the tone of their voice, and their want of energy and vigor, assimilate them more in appearance and

habits to the female than to the male type. If the testicles are removed nearer the period of puberty, or at any time after that term has occurred, and when the various male sexual peculiarities have been already developed, the effect is seldom so striking: the sexual instinct of the animals, and the energy of character which these instincts impart, are certainly more or less completely destroyed, and the tone of the voice is sometimes changed to that of puberty, but the general male character of form, such as the beard in man, and the horns of ruminants, generally continue to grow."

Darwin, after reviewing these facts, concludes as follows:

". . . We thus see that in many, probably in all cases, the secondary sexual characters of each sex lie dormant or latent in the opposite sex, ready to be evolved under peculiar circumstances.

"We can thus understand how, for instance, it is possible for a good milking cow to transmit her good milking qualities through her male offspring to future generations, for we may confidently believe that these qualities are present, though latent, in the males of each generation. So it is with the game-cock, who can transmit his superiority in courage and vigor through his female to his male offspring; and with man it is known that diseases necessarily confined to the male sex can be transmitted through the female to the grandson. Such cases are intelligible on the belief that characters common to the grandparent and the grandchild of the same sex are present, though latent, in the intermediate parent of the opposite sex."

Facts of this sort certainly seem, at first sight, to show the existence in each individual of two complete individualities, one from each parent; and the presence in each

sex, in a latent condition, of the organization of the other sex; but it is not difficult to show that the phenomena in question admit of a much simpler explanation.

In most cases when the sexes differ from each other in what are known as secondary sexual characteristics, that is, features which are not directly concerned in the reproductive function, the mature male is more different than the mature female from the young. I shall discuss this subject more fully in another place, so I shall give only a few illustrations at present. It will be sufficient to call attention to the resemblance between the smooth face of a woman and the face of either a boy or a girl, as contrasted with the bearded face of a man. The voice of a woman, the voice of a girl, and that of a boy, all resemble each other, and all differ from the voice of a man in the same, or nearly the same, respects.

In fowls the young of both sexes are much like the adult female in form and color.

These familiar instances are enough for our present purpose, and they show that, so far as the secondary sexual characteristics are concerned, the female is, as a rule, distinguished from the male by her failure to acquire the fully developed characteristics of the race. In these respects the female is an arrested male, and this is well shown by that fact that while the females and young of two closely related species of wild animals may be so much alike that they can hardly be distinguished, the adult males may be very different from each other.

All we need to assume, then, in order to reach a simple explanation of the secondary sexual differences between the sexes, is that each ovum has the power to develop into an organism with all the characteristics of the species, but that the female function acts, in some

way, to arrest the general organization somewhat short of full perfection.

We can also understand that the power to develop perfectly and to assume the characteristics of the sepcies might remain latent in the female, and might come into action after the loss of reproductive power.

According to this view, the possession of a beard must be regarded as a general characteristic of our race, inherited by all children, girls as well as boys. The development, in the girl, of the female reproductive function, or the lack of the stimulus which comes, in the male, from the development of the male function, arrests the development of the beard, although its power for growth may remain latent, and may come into more or less perfect activity after the period of reproduction is past.

A careful examination of the examples given above will bring out the interesting fact that when a female, from disease or mutilation or old age, assumes a resemblance to the male, the change is an advance, and consists in the acquisition of structures not usually present in the female. When, on the other hand, the male, from castration or confinement, comes to resemble the female, the resemblance is due, in most cases, to arrest, or a failure of the male to acquire the adult male characteristics of the species.

Simpson (*Hermaphroditism, Cyc. of Anat. and Phys.*, Vol. ii. p. 719) gives the following summary of the subject:

"The consideration of the various facts that we have now stated inclines us to the belief that the natural history characteristics of any species of animal are certainly not to be sought for solely either in the system of the male or in that of the female; but as Mr. Hunter pointed out, they are to be found in those properties that are

common to both sexes, and which we have occasionally seen combined together by nature upon the bodies of hermaphrodites, or evolved from the interference of art upon a castrated male or a spayed female.

"In assuming at the age of puberty the distinctive secondary peculiarities of his sex, the male, so far as regards these secondary peculiarities, evidently passes into a higher degree of development than the female, and leaves her more in possession of those characters that are common to the young of both sexes, and which he himself never loses when his testicles are early removed. These and other facts connected with the evolution of both the primary and the secondary peculiarities of the sexes farther appear to us to show that, physiologically at least, we ought to consider the male type of organization to be the more perfect, as respects the individual, and the female as respects the species. Hence we find that, when the female is malformed in the sexual parts so as to resemble the male, the malformation is almost always one of excessive development, and, on the other hand, when the male organs are malformed in such a manner as to simulate the female, the abnormal appearance is generally to be traced to a defect of development. In the same way, when the female assumes the secondary characters of the male it is either, first, when by original malformation its own ovaries and sexual organs are so defective in structure as not to be capable of taking a part in the function of reproduction, and of exercising that influence over the general organization which this faculty imparts to them; or, secondly, when in the course of age the ovaries have ceased to be capable of performing the action allotted to them in the reproductive process. In both of these cases we observe the powers of the female organization, now that its

capabilities for performing its particular office in the continuation of the species are wanting or lost, expend themselves in perfecting its own individual system, and hence the animal gradually assumes more or fewer of the secondary sexual characters that belong to the male."

It is true that, in a few instances, the male has been known to acquire true feminine characteristics, foreign to normal males. Thus, according to Darwin, "characteristics properly confined to the female are likewise acquired: the capon takes to sitting on eggs, and will bring up chickens; and what is more curious, the utterly sterile male hybrids from the pheasant and fowl act in the same manner, their delight being to watch when the hen leaves the nest, and to take on themselves the office of a sitter.

Many male birds normally sit, and hatch the eggs, and there are reasons for believing that the incubating habit was originally shared by both sexes, and I am therefore inclined to attribute such cases as this to reversion to a remote male ancestor, rather than to the acquisition by the male of a female characteristic.

We may conclude, then, that the transmission by one sex, in a latent condition, of the secondary characteristics of the opposite sex, does not compel us to believe in the dual sexual personality of each individual, since we have a much simpler explanation in the view that each embryo inherits the power to develop all the characteristics of the species, but that this power does not fully manifest itself in the female.

It may seem difficult to explain in this way the transmission by a bull of the good milking qualities of his mother, or the capacity occasionally shown by male mammals of yielding milk, but it is surely simpler to assume that each male inherits, like the females, the

power of developing perfect functional mammæ, and that this power is arrested in the male, than to assume that each male animal includes in itself a complete female duplicate.

An illustration may make the subject more clear. Certain embryo bees, when exposed to certain conditions, develop into sterile workers, but when exposed to another set of conditions they become fertile females. The differences between the workers and the queens are not confined to the reproductive organs, but extend to the shape and size of the body, the general organization, and to the instincts of the animals. These differences are not due to the direct action of the conditions to which the young are exposed, but are truly hereditary, as we see from the fact that the workers of different species are as distinct and as characteristic of their species as the male or the fertile females.

Now which is simplest, to assume that each female embryo has a complete worker organization and a complete queen organization, or to hold that it has the power to develop all the characteristics common to both, and also the distinctive characteristics of each; that one set of conditions suppresses the distinctive characteristics of a perfect queen, while another set of conditions arrests those of a perfect worker?

The argument in favor of the multiple personality of individuals which is furnished by polymorphic communities is at least as strong as that furnished by the latent transmission of secondary sexual characteristics.

In the case of the polymorphic hydroids an egg-embryo may give rise, by budding, to certain descendants with fully developed digestive organs, but with no organs of locomotion or reproductive organs, to other descendants with organs of locomotion, but without diges-

tive organs or reproductive organs, and to still others with reproductive organs, but with no organs of digestion or locomotion. All these forms are hereditary and are characteristic of the species, so there is no escape from the conclusion that they all are present in some form in the egg-embryo, and it is certainly natural to suspect that the entire organization of each one of them is latent in this embryo, but the explanation which I have proposed to account for the transmission of secondary sexual characteristics, applies to such cases as this just as well.

The hypothesis that the egg-embryo inherits and transmits to each of its descendants, those produced asexually as well as those produced sexually, all the characteristics of the species, and that it also inherits and transmits to each of them a tendency to suppress certain of these characteristics under certain conditions, seems to furnish a simple and satisfactory explanation of all the facts.

According to this view the feeding zooids of a polymorphic Siphonophore are individuals which have inherited in full all the characteristics of the race, but which do not attain to perfect development in all respects. The swimming zooids are similar individuals, with other characteristics suppressed, and so on.

This explanation seems much more satisfactory than the supposition that the egg-embryo contains one complete personality for feeding zooids, one for locomotor zooids and one for reproductive zooids, and I hope that this case will make clearer the lack of necessity for assuming the dual personality of each male or female animal, so long as we have a much simpler explanation in the hypothesis that each embryo has the power to develop all the characteristics of the species, together with a tendency to suppress certain ones in each sex.

A little thought will show that if there were no explanation of the transmission of latent sexual characteristics more simple than the hypothesis of a dual personality, this hypothesis would then be too simple, and would need to be made much more complicated.

The characteristics of the opposite sex are not the only ones which may be latent, and in cases of reversion a parent may transmit to children characteristics which were exhibited by neither parent nor grandparent, and which may have remained latent for many generations.

If we must assume the existence of a dual personality to account for the latent transmission of the characteristics of the grandparent of the opposite sex, we must assume still other personalities to account for reversion to more remote ancestors, and Darwin has not hesitated to carry the hypothesis to this, its logical conclusion.

He says (*Variation*, ii. 65), "Several authors have maintained that hybrids and mongrels include all the characteristics of both parents, not fused together but merely mingled in different proportions in different parts of the body; or, as Naudin has expressed it, a hybrid is a living mosaic work, in which the eye cannot distinguish the discordant elements, so completely are they intermingled. We can hardly doubt that, in a certain sense, this is true, as when we behold in a hybrid the elements of both species segregating themselves into segment in the same flower or fruit—by a process of self-attraction or self-affinity—this segregation taking place either by seminal or by bud propagation. Naudin further believes that the segregation of two specific elements or essences is eminently liable to occur in the male and female reproductive matter, and he thus explains the almost universal tendency to reversion in successive hybrid generations. . . . But it would, I suspect,

be more correct to say that the elements of both parent species exist in every hybrid in a double state, namely, blended together and completely separated."

In another place (*Variation*, ii. p. 80) he says: "On the doctrine of reversion, as given in this chapter, the germ becomes a far more marvellous object, for besides the visible changes to which it is subjected, we must believe that it is crowded with invisible characteristics, proper to both sexes, to both the right and left sides of the body, and to a long line of ancestors, male and female, separated by hundreds or even thousands of generations from the present time, and these characters, like those written on paper with invisible ink, all lie ready to be evolved under certain known or unknown conditions."

I shall discuss the phenomena of reversion somewhat at length in another place, and wish to simply call attention at present to the fact that here, as in the case of secondary sexual characters, we have a much simpler explanation in the hypothesis of arrest, and therefore do not need to call in an unknown factor, such as the multiple personality of each individual.

I think that the phenomena of alternation of generations favor this latter supposition even more than the facts of reversion.

The egg-embryo of a hydro-medusa may give rise by budding to an indefinite number of hydroids like itself, and each of these may give rise to other hydroids, and so on indefinitely.

Each one of these may also, under certain conditions, give rise to medusæ quite different from the hydroids and like the original medusæ. As the medusæ which are thus produced inherit through a long series of hydra ancestors all the specific characteristics of the origi-

nal medusa, we are forced to conclude that each hydroid contains, in a latent state, the power to reproduce a definite specific medusa.

As the hydra and its medusa differ from each other very much more than a male and a female mammal, and have little in common except the general plan of their organization, there seems at first to be no escape from the conclusion that the medusa structure exists side by side with the hydra structure, in each hydroid, as a second personality.

I hope to show, in the chapter on asexual reproduction that alternation of generations is a secondary condition of things, and that it has been brought about by a modification of ordinary metamorphosis.

I think there is every reason to believe that at one time the hydra-larva which hatched from a medusa egg became metamorphosed, by a gradual change during growth, into a medusa.

If this were the case now, there would be no more reason for believing in a hydra personality and a medusa personality than there is for believing that a human child contains a distinct adult personality.

Now we can understand that if such a larva should give rise by budding to other hydroids like itself, they also would have the power to grow into mature medusæ. We can also understand that circumstances might arise to cause the later stages in the development of some of these hydra-larvæ to become latent. We should then have two generations—hydroids without a medusa stage, and hydroids with a medusa stage.

The suppression of the hydra features of the latter would then give us a generation of medusæ with no hydra stage, giving birth to a generation of hydroids with no medusa stage, and these in turn producing a

generation of medusæ with no hydra stage. We should then have a case of alternation like that which is presented by ordinary hydro-medusæ.

Summary of Chapter.

A careful review of the reasons which have induced various authors to believe that either sexual element may transmit any characteristic whatever, leads to the conclusion that its truth is not proven.

It is impossible to prove it by the phenomena of crossing, since the only animals which can be made to cross are essentially alike, and differ only in minor points.

The homology between the ovum and the male cell is no reason for supposing that their functions are similar, and the differences between them should lead us to believe that their functions are not alike.

There is no reason for assuming that each sex transmits its entire organization to the offspring, in order to account for the latent transmission of secondary sexual characteristics, since this transmission can be more simply explained by assuming that each embryo inherits but does not necessarily develop all the characteristics of its species.

Reversion and alternation of generations admit of a similar explanation.

We may therefore conclude that there is and can be no proof that each sexual element transmits all the characteristics of the parent, and that there is no *a priori* absurdity in the hypothesis that the male and female reproductive elements are unlike in function, and are specialized in different directions.

We can therefore enter without prejudice into an examination of the evidence for this latter view.

CHAPTER VI.

THE EVIDENCE FROM HYBRIDS.

Importance of the subject—It furnishes a means of analyzing or isolating the influence of each sexual element—Hybrids very variable—Hybrids from domesticated races more variable than those from wild races—The descendants of hybrids more variable than the hybrids themselves—The offspring of a male hybrid and the female of a pure species are much more variable than those of a female hybrid and the male of a pure species—These facts inexplicable on any view, except the one here presented—Reciprocal crosses—They differ in fertility and in structure—The difference is exactly what our theory requires—Difficulty in explaining transmission of characters without fusion—Reversion caused by crossing—Two kinds of reversion—Summary.

THE study of hybrids and crosses is of especial interest to us, since it affords us a means, somewhat imperfect it is true, for recognizing, in the offspring, the structure which it owes to each parent.

In ordinary sexual reproduction between animals or plants of the same race, the parents are almost exactly alike, except for their sexual differences; and as nearly every structural feature of the young is a feature of resemblance to each parent, there can be nothing to show that it is inherited from the one rather than from the other.

When distinct races or species are crossed, the case is somewhat different. It is true that the two parents are still very much alike, for species cannot be made to breed together at all unless they are very closely related. Still they are more different from each other than individuals

of the same species, and the study of crosses and hybrids is therefore a means of separating, to some extent, the influence of one parent from the influence of the other. This is true, however, only with reference to characteristics which are of recent acquisition, for the greater part of the history of two allied species has been the same, and they show in common everything except what has been acquired by each one since they diverged from their common ancestor.

Crossing gives no way of showing whether these common characteristics are or are not transmitted by one parent or the other or by both, but it does give us this information regarding characteristics which appear in one species but not in the other, and it is therefore the best means at our disposal for studying the influence of each parent upon the offspring.

Crossing as a Cause of Variation.

According to our theory of heredity, we can easily see how the crossing of two species or varieties should lead to variability, for when two species or varieties are crossed certain cells of the body will be hybrids between the gemmules of the male parent and the ovarian particles inherited through the female from the egg of the preceding generation. Now the ovarian particle transmits the properties of a cell like that of the female parent, while the gemmule transmits those of a corresponding cell in the father. It is plain that corresponding cells of a female of one species or variety and of a male of another species or variety must be more different from each other than corresponding cells in a male and female of the same species or variety. The hybrid cell formed by their union would, therefore, be expected to differ more from each of them, that is, to vary more than it

does in the offspring of parents of the same variety. It is well known that this is the case; that, in domesticated animals and plants at least, crossing is a great cause—according to some older writers the only cause—of variation.

Darwin says that it is probable that the crossing of two forms when one or both have long been domesticated or cultivated, adds to the variability of the offspring, independently of the commingling of the characters derived from the two parent forms. He believes that new characters arise in this way in hybrids between domesticated forms, forms which have been rendered variable through cultivation, but he doubts whether we have, at present, sufficient evidence to prove that the crossing of species which have never been cultivated leads to the appearance of new characters.

The following illustrations of this law are quoted from his *Variation* (Vol. ii. p. 319):

"Gärtner declares, and his experience is of the highest value on such a point, that when he crossed native plants which had not been cultivated, he never once saw in the offspring any new character; but that from the odd manner in which the characters derived from the parents were combined, they sometimes appeared as if new. When, on the other hand, he crossed cultivated plants, he admits that new characters occasionally appeared. . . . According to Kölreuter, hybrids in the genus Mirabilis vary almost infinitely, and he describes new and singular characters in the form of the seeds, in the colors of the anthers, in the colyledons being of immense size, in new and highly peculiar odors, in the flowers expanding early in the season, and in their closing at night. With respect to one lot of these hybrids he remarks that they presented characters exactly the reverse

of what might have been expected from their parentage.

"Professor Lecoq speaks strongly to the same effect in regard to this same genus, and asserts that many of the hybrids from Mirabilis jalapa and multiflora might easily be mistaken for distinct species, and adds that they differed in a greater degree than the other species of the genus from M. jalapa. Herbert has also described the offspring from a hybrid Rhododendron as being as unlike all others in foliage as if they had been a separate species. The common experience of floriculturists proves that the crossing and recrossing of distinct but allied plants, such as the species of Petunia, Calceolaria, Fuchsia, Verbena, etc., induces excessive variability: hence the appearance of quite new characters is probable. M. Carriere has lately discussed this subject; he states that Erythrina cristagalli had been multiplied by seed for many years, but has not yielded any varieties; it was then crossed with the allied E. herbacia, and the resistance was now overcome, and varieties were produced with flowers of extremely different size, form, and color."

Darwin, therefore, concludes that crossing, like any other change in the conditions of life, seems to be an element, probably a potent one, in causing variability.

The variability of hybrids is quite as explicable by Darwin's Pangenesis hypothesis as it is by our theory of heredity, although I do not see why, on the hypothesis of pangenesis, the hybrid offspring of domesticated forms should be any more variable than those produced between wild species.

The Offspring of Hybrids more variable than the First Generation

There is another aspect of the variability of hybrids which is very remarkable, and which is in perfect agreement with our theory of heredity, but, so far as I am aware, absolutely inexplicable without it.

This is the law that although the offspring of the first generation are generally uniform when two species or races are crossed, the subsequent generations of children produced by these hybrids display an almost infinite diversity of character. (Darwin, *Variation*, ii. p. 321.)

Darwin also refers to this curious law in the Origin of Species, p. 260, and attempts an explanation of it. He says: "The slight variability of hybrids in the first generation, in contrast with that in the succeeding generations, is a curious fact, and deserves attention. For it bears on the view which I have taken of one of the causes of ordinary variability, namely, that the reproductive system from being eminently sensitive to changed conditions of life, fails under these circumstances to perform its proper function of producing offspring closely similar in all respects to the parent form. Now, hybrids in the first generation are descended from species (excluding those long cultivated) which have not had their reproductive systems in any way affected, and they are not variable; but hybrids themselves have their reproductive systems seriously affected, and their descendants are highly variable."

According to this view, the variability of the descendants of hybrids is a sort of monstrosity, due to the failure of the reproductive organs to perform their proper functions; ordinary variability is not monstrosity, but is perfectly normal, and as the variability of hybrids

has precisely the same character, I think we cannot regard it as due to unnatural disturbance.

According to our theory, variation is due to the action of changed or unnatural conditions upon certain cells of a preceding generation. Now, as characteristics of both parents are mingled in a hybrid, it must nearly always happen that certain cells with peculiarities of one parent will be in contact with, or will depend in some way upon, cells with peculiarities inherited from the other species. There will therefore be a lack of the perfect adjustment between each cell and its neighbors, which has been brought about in each parent by natural selection, and this imperfect adjustment will cause the cell which is unfavorably placed to throw off gemmules. The cells of the body of a hybrid will therefore be unusually prolific of gemmules, and will transmit variability to later generations.

According to our hypothesis, a hybrid is more likely to transmit variability than a pure species, because more of its cells are placed under circumstances favorable to the production of gemmules.

For the same reason a hybrid between two domesticated or cultivated forms must have more tendency to vary than one produced by crossing two wild species, for the domestic or cultivated parents live under unnatural conditions, and therefore have more tendency than wild species to transmit gemmules, and thus cause variability.

The Sex of the Parent affects the Variability of Hybrids.

I have shown that the body of a hybrid is peculiarly favorable for the production of gemmules, and that, for this reason, the descendants of hybrids are variable

to an unusual degree. Now, if our theory of heredity is true, if the seminal fluid is especially adapted for the transmission of gemmules, while their transmission by an ovum is a matter of accident, the tendency to vary must be transmitted by the male hybrid.

When children are born from two hybrid parents it is impossible to show that the variability which follows comes from the father rather than from the mother, but the subject can be put to a test by crossing the male hybrid with a female of one of the pure species, and the male of one of the pure species with the female hybrid. Neither pure species has any especial tendency to transmit variation, while the male hybrid has such a tendency. If, then, we cross the female hybrid with the male of one of the pure forms, the offspring would not be expected to be unusually variable; but if the male hybrid is crossed with one of the pure females we should expect the offspring to be unusually variable.

Now it is very interesting to find that this actually is the case. Thus Gärtner states (*Bastarderzeugung*, p. 452, 507) that when the seeds of Dianthus barbatus were fertilized by the pollen of the hybrid Dianthus chinensi-barbatus, the seedlings were more variable than those which were raised from the seeds of the hybrid fertilized with the pollen of Dianthus barbatus. Darwin states that Max Wichura obtained the same result with willows. Gärtner concludes from a number of experiments that when a hybrid is used as the father, and either one of the pure parent species or a third species as the mother, the offspring are more variable than when the same hybrid is used as the mother, and either pure parent or the third species as the father.

Darwin's pangenesis hypothesis furnishes no explanation whatever of this curious fact. On the contrary, as

it requires that each sexual element should contain gemmules from every part of the body of the parent, it is directly opposed to any such result, and there is no place for it in any other hypothesis of heredity. Our theory fits it exactly, however, and a more crucial test could hardly be proposed than an experiment like those detailed by Gärtner.

Reciprocal Hybrids.

According to Darwin the two sexes play similar parts in heredity, and any characteristic whatever may be transmitted by either sexual element.

This conclusion is based upon the phenomena of crossing, but a little thought will show that it is impossible, from the nature of the case, to prove it from evidence of this kind, although, as I hope to show, it is capable of disproof.

Only animals of the same species, or of closely related species, can breed together. Closely allied animals are alike in all respects, except as regards the slight differences which distinguish species, varieties and individuals from each other. Since no animals or plants can cross except those which have most of their past history in common, and which are therefore alike in nearly every respect, it is plainly impossible to prove, from the phenomena of crossing, that each parent has power to transmit the features which are sharèd by the other parent as well. The phenomena of parthenogenesis, or reproduction by virgin females, as in the case of bees and wasps, show that the ovum alone may transmit all the established hereditary structure of the species, but there is and can be no evidence to show that the male element can accomplish the same thing.

The facts of crossing, while they cannot prove that the

functions of the two reproductive elements are alike, do furnish convincing proof of the contrary, and show that they are not alike.

A reciprocal cross is a double cross between two species or varieties, one form being used in one case as the father, and in the other case as the mother. Thus a reciprocal cross between a horse and an ass is a double cross, between the male horse and the female ass on the one hand, and the female horse and male ass on the other.

Now, if it is true that the function of the ovum is like that of the male cell, the offspring of reciprocal crosses should be alike in all respects, but this is by no means the case.

In the first place, the degree of sterility often differs greatly in two species when reciprocally crossed; for the male of the first will, in some cases, readily fertilize the ovum of the second, and thus give rise to descendants; while hundreds of attempts to fertilize the ovum of the first by the male of the second, result in uniform failure. It often happens also that even when both crosses result in the production of offspring, the hybrid in the one case is sterile, while in the other case it is perfectly fertile.

Not only do the results of reciprocal crossing show this difference, but they show what is still less reconcilable with the view that the functions of the sexual elements are alike, namely, great differences of structure.

In some cases where a reciprocal cross is perfectly fertile on both sides, the hybrids which are thus produced are not at all alike. When the male of species A and the female of B are crossed, the offspring is an entirely different being from the one born from A as a mother with B as a father.

We know that allied species of animals are the descend-

ants of a common ancestral form, from which they inherit all that they have in common, while the distinctive peculiarities which distinguish them from each other are more recently acquired.

According to our hypothesis the ovum transmits established characteristics, while the cells which have recently varied in the body of the male transmit gemmules.

If, then, we select two allied species or varieties and cross the male of one with the female of the other, and then, reversing the process, cross the female of the first form with the male of the second, we should expect to find, in many cases, a difference in the offspring. Where the male of species or variety A is crossed with the female of B, the offspring will inherit from its mother the common characteristics of both parents, and it will also receive from its father gemmules from those cells which have recently varied in the species A. The corresponding cells of its body will therefore be hybrids, and will bear a closer resemblance than the other parts of its body to the species A. That is, the hybrid will share, to some extent, the peculiarities which are distinctive of the species A as compared with B. The offspring of the opposite cross will, on the other hand, join, more or less perfectly, to the common race characteristics, some of the distinctive peculiarities of the species A produced in it by the hybridization of the cells of its body by gemmules received from its father.

Reciprocal crosses between the horse and the ass have been reared for domestic purposes for ages, and Huxley gives the following interesting account of the result:

"The offspring of the ass and the horse, or rather of the he-ass and the mare, is what is called a mule; and, on the other hand, the offspring of the stallion and the

she-ass is what is called a hinney. It is a very rare thing in this country to see a hinney. I never saw one myself; but they have been very carefully studied. Now the curious thing is this, that although you have the same elements in the experiment in each case, the offspring is entirely different in character, according as the male influence comes from the ass or the horse. When the ass is used as the male, as in the case of the mule, you find that the head is like that of the ass, that the ears are long, the tail is tufted at the end, the feet are small, and the voice is an unmistakable bray; these are all points of similarity to the ass; but, on the other hand, the barrel of the body and the cut of the neck are much more like those of the mare. Then if you look at the hinney—the result of the union of the stallion and the she-ass—then you find it is the horse which has the predominance; that the head is more like that of the horse; the ears are shorter, the legs coarser, and the type is altogether altered, while the voice, instead of being a bray, is the ordinary neigh of the horse. Here, you see, is a most curious thing; you take exactly the same elements, ass and horse, but you combine the sexes in a different manner, and the result is modified accordingly."

It would certainly be a wonderful thing if the combination of the same elements should give such different results, and I think we must conclude that the elements are not the same, but that the ovum and the male cell do not play the same parts in heredity.

There are not many cases in which reciprocal crosses have been made so frequently, and single observations are not of very great value. I will, however, cite a few, to show that the one given is not exceptional. The Manx cat is a variety of the domestic cat peculiar to the Isle of Man. It differs from the ordinary cat in having no tail,

and in some other slight peculiarities; its hind legs are longer, and its habits peculiar. According to Mr. Orton (Physiology of Breeding, 1855, p. 9; quoted by Darwin, *Variation*, ii. 86), Dr. Wilson crossed a male Manx cat with common cats, and, out of twenty-three kittens, seventeen were destitute of tails; but when the female Manx was crossed by common male cats all the kittens had tails, though they were generally short and imperfect. Darwin gives the following in his Variation under Domestication (ii. 85): "Godina has given a curious case of a ram of a goat-like breed of sheep from the Cape of Good Hope, which produced offspring hardly to be distinguished from himself when crossed with ewes of twelve other breeds. But two of these half-bred ewes, when put to a merino ram, produced lambs closely resembling the merino breed."

I quote the following from Darwin also (p. 87): "The silk fowl breeds true, and there is reason to believe that it is a very ancient race; but when I reared a large number of mongrels from a silk hen by a Spanish cock, not one exhibited even a trace of the so-called silkiness. Mr. Hewitt also asserts that in no instance are the silky feathers transmitted by this breed when crossed with any other variety. But three birds out of many raised by Mr. Orton from a cross between a silk cock and a bantam hen had silky feathers.

There are some instances of reciprocal crosses which seem at first sight to give directly opposite results, and therefore to contradict our theory.

Thus Darwin says that a hybrid which had for its mother a bay mare and for its father a hybrid between a male ass and a female zebra, had, when young, zebra-like stripes upon its shoulders, flanks and legs. Here the only recent striped ancestor is the paternal grand-

mother. As the possession of stripes is a characteristic which distinguishes the zebra from the horse and the ass, it seems at first as if its transmission by a female ancestor is opposed to our theory. We know, however, that all the species of the horse genus are the descendants of a striped form, and the presence of stripes in the zebra is not due to recent variation, but to the fact that it has not varied. The transmission of stripes by a female zebra is therefore nothing more than we might expect. We know, too, that both the horse and the ass show a tendency to revert to the striped ancestral form, and I shall show in the next section that reversion is often excited by crossing. It is therefore quite probable that the stripes in this colt were due to reversion.

It is said that young animals born from a tigress by a male lion, as well as those born from a lioness by a male tiger, are striped, but many cat-like animals show a tendency to revert to a striped form, and in this case also we may explain the presence of stripes in the young by attributing it to reversion excited by crossing.

Darwin says that a good authority assures him that in South America, when niata cattle are crossed with common cattle, though the niata is prepotent whether males or females are used, the prepotency is strongest through the female line.

The origin of the niata breed is not known, but there is no doubt that it originated in Paraguay from common cattle; and the fact that the niata peculiarities are not shared by any other living cattle, but are very much like those of the extinct Sivatherium, seems to show that in this case also the peculiarity is due to reversion.

Difficulty of Explaining the Transmission of the Characters of Two Forms without Fusion.

A much more serious difficulty is found in the fact that while a hybrid is usually somewhat intermediate between its parents, it occasionally happens that the characteristics of one or both parents refuse to blend and are transmitted in an unmodified state. Thus Darwin states that when gray and white mice are paired the young are not piebald nor of an intermediate tint, but are pure white or of the ordinary gray color. This particular case may perhaps be explained as follows: The brown form is the ancestral form, and when no hair gemmules are transmitted the young are brown. All the hairs are homologous with each other, and are derived from the same part of the egg, and when gemmules are transmitted they may hybridize alike all the cells which are to form hairs, and the hybrid animals will therefore be entirely white or entirely brown.

It is stated that when a black game fowl is crossed with a white, the young are either pure black or pure white. but this case is precisely like that of the mice.

Darwin gives a number of interesting illustrations of this singular phenomenon, among which are the following:

When turnspit dogs and ancon sheep, both of which have dwarfed limbs, are crossed with common breeds, the offspring are not intermediate in structure, but resemble one parent only.

When tailless or hornless animals are crossed with perfect animals, it frequently but by no means invariably happens that the offspring are either perfectly furnished with these organs or are quite destitute of them.

When Dorking fowls with five toes are crossed with

other breeds, the chickens often have five toes on one foot and four on the other.

When the red flowered stock of Antirrhinum is fertilized with the pollen of the purple Queen stock, about half the seedlings resemble the mother plant, while the other half bear rich purple blossoms like those of the paternal plant.

Darwin says that he fertilized the purple sweet-pea, which has a dark reddish-purple standard-petal and violet-colored wings and keel, with pollen of the painted-lady sweet-pea, which has a pale cherry-colored standard and almost white wings and keel, and from the same pod twice raised plants resembling both sorts, the greater number resembling the father.

These cases are difficult to explain, but the phenomena are so complicated that it is hardly safe to speculate upon them until they are re-examined by an observer who can devote himself to this subject especially.

Some of them may be due to the causes above indicated, and some, possibly, to fertilization by two fathers.

Crossing as a Cause of Reversion.

According to Darwin's view reversion must in all cases be due to the manifestation of a tendency which has lain dormant in the egg and has been transmitted for generations in a latent condition, for the chances against the repetition, by an accidental variation, of a characteristic of a remote ancestor, are inconceivably great.

According to our theory this is not the case, for the conditions which caused a cell in the ancestral form to throw off gemmules and thus to produce a given peculiarity may cause the corresponding cell of the parent to throw off gemmules in the same way, and these, uniting with the corresponding part of the egg, will produce

variation. As the gemmule and the ovarian element are both very similar to those which produced the variation in the ancestor, the chances are not very great against the reproduction of the same peculiarity. In this case we should have a new variation with all the characteristics of a true reversion, but due to the transmission of a gemmule, rather than to the sudden awakening of a tendency which has long lain dormant in the egg.

It is possible, therefore, that there may be two kinds of reversion—true hereditary reappearance of features which have lain latent in the egg, and new variations which repeat again certain old characteristics of the race. There are, I think, certain reasons for believing that reversions of the latter kind are the most common, the chief one being the fact that most of the causes of variability are also causes of reversion.

Thus, crossing, which is a very efficient cause of variation, is also one of the chief causes of reversion.

Darwin gives a number of examples to show that, independently of the well-known tendency of hybrids and mongrels to revert, after a number of generations, to one of the parent forms, the act of crossing in itself gives an impulse towards reversion, and often results in the reappearance of long-lost characters.

The following interesting account, from Darwin's *Variation* (Vol. ii. p. 57), will serve to illustrate this law:

"In the chapter on the horse, reasons were assigned for believing that the primitive stock was striped and dun colored, and details were given showing that in all parts of the world stripes of a dark color frequently appear along the spine, across the legs and on the shoulders, where they are occasionally double or treble, and even sometimes on the face and body of horses of all breeds and of all colors. But the stripes appear most

frequently on the various kinds of dun. They may sometimes plainly be seen on foals and subsequently disappear.

"The dun color and the stripes are strongly transmitted when a horse thus characterized is crossed with any other, but I was not able to prove that striped duns are generally produced from the crossing of two distinct breeds, neither of which are duns, although this does sometimes occur.

"The legs of the ass are often striped, and this may be considered as a reversion to the wild parent form, the *Asinus tæniopus* of Abyssinia, which is thus striped. In the domestic animal the stripes on the shoulder are occasionally double or forked at the extremity, as in certain zebrine species. There is reason to believe that the foal is frequently more plainly striped on the legs than the adult animal. As with the horse, I have not acquired any distinct evidence that the crossing of differently colored varieties of the ass brings out the stripes.

"But now let us turn to the result of crossing the horse and ass. Although mules are not nearly so numerous in England as asses, I have seen a much greater number with striped legs, and with the stripes far more conspicuous than in either parent form. Such mules are generally light-colored, and might be called fallow-duns. The shoulder stripe in one instance was deeply forked at the extremity, and in another instance was double, though united in the middle. Mr. Martin gives a figure of a Spanish mule with strong zebra-like marks on its legs, and remarks that mules are particularly liable to be thus striped on the legs. In South America, according to Roulin, such stripes are more frequent and conspicuous in the mule than in the ass. In the United States, Mr. Gosse, speaking of these animals, says that in a great

number, perhaps in nine out of every ten, the legs are banded with transverse dark stripes."

Mules with striped legs can be seen in great numbers every day in the streets of Baltimore, and the peculiarity is not in the least uncommon.

Darwin gives a number of cases in which the same reversion has been produced by the crossing of other horse-like forms, and we must regard the tendency to revert to a striped form when crossed as characteristic of the horse family.

Darwin says that when he crossed different varieties of fowls he often got birds with faint traces of the peculiar red plumage of the wild *Gallus bankiva,* and that this plumage was almost perfectly reproduced in one magnificent bird, the offspring of a black Spanish cock and a white silk hen, although either of these pure breeds may be reared by tens of thousands without the appearance of a single red feather.

Even long-lost instincts may be made to reappear by crossing. The original wild ancestor of our domestic fowls must, like all wild incubating birds, have had the incubating instinct. Now when two non-sitting breeds of fowls are crossed, the mongrels frequently recover their incubating habit and sit with remarkable steadiness.

It is said that hybrids between perfectly tame domestic animals are often as wild as their wild ancestors. This has been noticed in cattle, pigs, fowls, ducks, and it is probable that the same thing frequently shows itself when widely separated human races are crossed, as such good authorities as Livingston and Humboldt have remarked upon the savage character of half-caste human beings.

Another interesting resemblance between reversion and

ordinary variation is the fact that the descendants of hybrids are more apt to revert than the hybrids themselves. Darwin says (Variation, p. 65) that this is a general rule.

Now, whether reversion be due to the sudden excitement of a tendency which has long been transmitted in a dormant state by the ova, or whether it is due to the appearance of a new variation which resembles an old one, we can readily understand how, according to our theory of heredity, crossing should call this power into action. During the evolution of the species each hereditary peculiarity has been established in the egg by gemmules, and anything which prevents the egg from following its normal course and developing the recently acquired characteristics of the species, would allow older characteristics to appear in their place.

We know that animals which are very widely separated are infertile, and we can understand that even when the difference between two species is not great enough to prevent them from crossing, those cells of their bodies which have varied most may be so different from each other that gemmules from the one cannot fertilize the egg-particles which are to produce the other, or when they do fertilize them they may give rise to a variation which is so different from the normal cell that it cannot live. The cells which precede these in the order of growth being less different in the two parents, would be much more favorably situated, and would thus give to the embryo a characteristic of longer standing than the peculiarities of either parent. On the other hand, if reversion is simply variation, we can see that crossing might excite reversion just as it excites variability.

Summary of Chapter.

The study of hybrids gives us a means of comparing, within certain narrow limits, the parts which the two sexual elements play in heredity. The influence of each sex can, in a certain sense, be studied by itself when a given species is used in the one case as the father of a hybrid, and in another case as the mother. The value of crossing as an experiment in heredity is greatly limited, however, by the fact that, although we can study the influence of one sexual element unobscured by the other element from the same species, it is obscured and complicated by the influence of this element from an allied species, and in all organisms which can breed together the reproductive elements must be essentially alike.

Hybrids do, however, present a number of peculiarities which agree perfectly with what we should expect according to our hypothesis, and certain of these are inexplicable without it.

Hybrids and mongrels are highly variable, as we should expect to be the case, according to Darwin's pangenesis hypothesis. This hypothesis fails to account for the fact that hybrids from forms which have long been domesticated are more variable than those from wild species or varieties, or for the very remarkable fact that the children of hybrids are much more variable than the hybrids themselves.

Our theory not only explains the variability of hybrids, but it also accounts for the two latter peculiarities, for crossing will not give rise to a marked or conspicuous variation unless the hybrid inherits numbers of gemmules, and as domesticated animals and plants live under unnatural conditions they are more favorably placed than wild forms for the production of gemmules.

The body of a hybrid is in itself a new thing, and therefore in a certain sense unnatural, and a male hybrid is, accordingly, more fitted for the production of gemmules than a male of a pure or unmixed race.

When a male hybrid is crossed with the female of either pure species or with a third species, the children are much more variable than those born from a hybrid mother by a male of a pure species. It would be difficult to devise an experiment better fitted than this to show that variation is caused by the influence of the male, and that the action of unnatural or changed conditions upon the male parent results in the variability of the child.

The remarkable history of reciprocal hybrids is directly opposed to Darwin's view that the functions of the two reproductive elements are essentially similar, for in some cases it is impossible to breed from a female of one species by the male of a second species, while the male of the first species readily fertilizes the ovum of the second and gives rise to fertile offspring. Even when both crosses are fertile the one is often much more so than the other.

The hybrids of one cross often differ remarkably from those of the other cross in general structure, and in many cases they show, in addition to the common characteristics of both parents, a tendency, more or less perfectly pronounced, to develop the recently acquired characteristics of that species which is used as the father.

This law is often obscured by the appearance of reversions, which are peculiarly apt to occur in hybrids, and by the presence, in certain cases, of a tendency for each parent to transmit its peculiarities to the hybrid, without fusion with those of the other parent. But when we

consider the great obscurity and complexity of the case, and the great difficulty in conducting rigid experiments, the balance of the evidence from hybrids seems to be greatly in favor of our view of the nature of heredity. It certainly presents features which are inexplicable in any other way, and perfectly simple and natural if our view is accepted.

CHAPTER VII.

THE EVIDENCE FROM VARIATION.

Causes of variation—Changed conditions of life induce variability—No particular kind of change is necessary—Variability is almost exclusively confined to organisms produced from fertilized ova—Bud variation very rare—History of the Italian orange—The frequency of variation in organisms produced from sexual union, as compared with its infrequency in those produced asexually, receives a direct explanation by our theory of heredity—Bud variation more frequent in cultivated than in wild plants—Our theory would lead us to expect this—Changed conditions do not act directly, but they cause subsequent generations to vary —Tendency to vary is hereditary—These facts perfectly explicable by our theory—Specific characters more variable than generic—Species of large genera more variable than those of small genera—A part developed in an unusual way highly variable—Law of equable variation—Secondary sexual characters variable—Natural selection cannot act to produce permanent modification unless many individuals vary together—Our theory is the only explanation of the simultaneous variation of many individuals—This theory also simplifies the evolution of complex structures—Saltatory evolution—This is explained by our theory of heredity —Correlated variation of homologous parts—Parts confined to males more variable than parts confined to females—Males more variable than females—Summary of last two chapters.

The Causes of Variation.

CERTAIN authors have held that variability is a necessary accompaniment of reproduction; that it is determined by something within rather than without the or-

ganism, but Darwin, after long and careful study of the subject, reaches the conclusion that each variation is excited by a change of some kind in the environment. It is impossible to expose animals for any length of time to absolutely uniform conditions, and we therefore find that when careful attention is given to the subject, minute individual differences may be detected in animals which are apparently most uniform. A shepherd easily learns to recognize each sheep in a large flock, and ants are able to perceive a difference between the members of their own community and those from another nest.

It is impossible to show by direct proof that uniform conditions of life would prevent variation; but it is quite possible to approach the subject from the other side, and to show that slight external changes cause slight variability, and greater changes greater variability.

Wild animals and plants vary somewhat and have individual peculiarities, for each one is under slightly different relations to the external world from all the others, but as compared with domesticated species their conditions of life are very uniform.

A wild animal has become habituated to the circumstances under which it lives, by exposure, for generations after generations to the action of natural selection, and a host of competing animals tend to keep it in its place, but domesticated animals are protected from their enemies and competitors, they are removed from their natural conditions, and they are frequently carried from their native land and are exposed in other countries to unnatural food and climate. They are compelled to change their habits, and they are never left long at rest, or exposed for any considerable length of time to closely similar conditions, but they are carried from dis-

trict to district, and their food and treatment varies considerably.

We accordingly find that, with few exceptions, all our domesticated animals and plants vary more than their wild relations. Even the goose, one of the least variable of domesticated animals, varies more than almost any wild bird, and according to Darwin, hardly a single plant can be named, which has long been propagated and cultivated by seed, that is not highly variable.

These considerations force us to conclude that variability is not a necessary contingent of reproduction, but that the production of the gemmules which give rise to variation is excited by changes in external conditions, and we must agree with Darwin that "it is probable that variability of every kind is directly or indirectly caused by changed conditions of life; or to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability."

When we come to examine the effect of different conditions of life we find that we cannot attribute the variability to one rather than the other. The essential thing is change, but not any particular kind of change.

Variation is frequently caused by a change of climate, but this is by no means essential, for most cultivated plants yield more varieties when cultivated in their native country than when removed to other climates. (Darwin, *Variation*, ii. p. 310.)

Change of food is often a cause of variation, but that this is not necessary is shown by the fact pointed out by Darwin, that fowls and pigeons are the most variable of domesticated animals, although their food is nearly the same as that of their wild allies, but is much less varied

than that which they would find for themselves in a state of nature.

Excess of food often causes variation, yet the turkey and goose have been encouraged and tempted for generations to feed to excess, and they have varied but little.

These examples show that the character of the change is unimportant, and that variability cannot be attributed to the exclusive influence of any particular class of external conditions; that the exciting cause of variation is change, but not any particular kind of change.

Darwin quotes a number of cases to show how slight a change may result in variability.

Thus the wild horses of the pampas of South America are of one of three colors, and the wild cattle are of one color; but when the same horses and cattle are domesticated, although they are not confined, but are allowed to run at large like the wild forms, they entirely lose their similarity of color, and display the greatest diversity in this particular. In India several species of fresh-water fishes are reared in great tanks as large as natural ponds, and they are all very variable. Darwin quotes from Downing the statement that varieties of the plum and peach which breed truly by seed, lose this power, and like other worked trees give variable seedlings when grafted on another stock.

Variability almost Exclusively Confined to Organism Produced from Fertilized Ova.

The only method open to us besides the study of hybrids for observing the influence of the sexes in heredity, is by a comparison of sexual with asexual heredity. As I shall show in another place, all the various forms of asexual reproduction are so connected that we may pass from fission, or the formation of two new organisms

by the splitting of one old one, to parthenogenesis, or reproduction from unfertilized ova, without finding any important gap in the series, and we may safely conclude that all these forms of reproduction are fundamentally alike.

So far as regards the physical side of the problem of heredity, the only essential difference between asexual reproduction and sexual reproduction is the absence of fertilization or union with a male cell in the one case, and its occurrence in the other case.

It is therefore extremely important to compare the two processes, in order to discover whether this physical difference is accompanied by any difference in the result. In the one case we have heredity with the male factor omitted, and in the other we have heredity with a male factor, and if there is any constant difference in the result, we may safely attribute it to this factor.

In making this comparison we are almost compelled to restrict ourselves to plants, for although asexual reproduction is not at all unusual in animals, it is restricted, with one exception, to animals which are not domesticated or reared by man, and we therefore know too little about the minute details of their life to make use of them for our purpose. The number of plants which have been cultivated and carefully observed and studied by man is very great, and as most of them multiply asexually by budding, as well as by fertilized seeds, we here have abundant material for comparative study, and it is well established by hundreds of thousands of observations that the presence or absence of the influence of the male element does have an influence upon the result of the reproductive process, and that this result is exactly what our view of the nature of the process would lead us to expect. Plants produced from fertilized seeds differ from those

produced from buds only in their greater tendency to vary. Bud variations do occur, but they are very unusual, while more or less variation in seedling plants is almost universal.

As we suppose that any cell may, when excited by unfavorable conditions, throw off gemmules, the gemmules may find their way, by a sort of accident, to growing buds, and thus cause variation. We should therefore expect bud variation to occur occasionally, but very much less frequently than variation in seedlings.

This is so well known to be the case that many authors have held that there can be no variation without sexual union. Darwin has shown, however, by a long list of instances of bud variation in plants, that this is not absolutely true, and the weight of his authority has led to the almost universal acceptance of his conclusion that there is no essential difference between asexual and sexual heredity. I shall discuss this conclusion at length in another place, as I believe that the facts demand an interpretation which is somewhat different from the one which Darwin furnishes. At present I simply wish to call attention to the fact that all authorities agree that variation is almost infinitely more common in sexual than it is in asexual offspring.

Asexual multiplication in animals is restricted to the lower forms which are of little use to man, and as these forms have not been domesticated and carefully observed, our knowledge of the variability of organisms produced asexually is almost entirely derived from the study of plants.

The only instance in domesticated animals of anything like asexual reproduction is the parthenogenetic reproduction of bees, and it is therefore interesting to note

that the hive-bee is the least variable of all domesticated animals (Darwin, *Variation*, Vol. ii. p. 307).

Darwin says (*Variation*, Vol. i. p. 360) that he procured a hive full of dead bees from Jamaica, where they have long been naturalized, and on carefully comparing them under the microscope with his own bees, could not detect a trace of difference.

With plants it is well known to all cultivators that forms which are highly variable as seedlings can be kept perfectly true by asexual propagation, and we have Darwin's authority (*Variation*, Vol. ii. p. 307, and Vol. i. p. 429) for the statement that while hardly a single plant can be named which has long been cultivated and *propagated by seed* that is not highly variable, the total number of instances of bud variation *is as nothing* in comparison with seminal varieties.

This contrast is the more remarkable when we recollect that in most of our cultivated plants the number of buds which develop is thousands of times greater than the number of seeds which give rise to plants. It is clear that if the chance of variation were the same in both cases the number of bud variations would be thousands of times greater than the number of seedling variations. If there were thousands of chances of seedling variation for one chance of bud variation, the number of bud varieties would still be equal to the number of seedling varieties.

The fact that with all this probability in their favor, bud varieties are very rare as compared with seedling varieties, shows that the chance of bud variation is almost infinitely small as compared with the chance of seedling variation.

While we cannot deny that variation may sometimes occur in organisms produced asexually, I think we are

justified in giving great emphasis to the law that variability is almost exclusively the characteristic of organisms produced from fertilized ova.

Darwin says (*Variation*, Vol. ii. pp. 351 and 377), "When we reflect on the millions of buds which many trees have produced before some one bud has varied, we are lost in wonder what the precise cause of each variation can be." "Habit, however much prolonged, rarely produces any effect on a plant propagated by buds: it apparently acts only through successive seminal generations."

The curious history of the naturalization of the orange in Italy, quoted by Darwin on the authority of Gallesio (*Theoria della Riproduzione Veg*, 1816, p. 125), is very interesting in this connection. During many centuries the sweet orange was propagated exclusively by grafts, and so often suffered from frost that it required protection. After the severe frost of 1709, and more especially after that of 1763, so many trees were destroyed that seedlings from the sweet orange were raised, and to the surprise of the inhabitants their fruit was found to be sweet. The trees thus raised were larger, more productive and hardier than the former kinds, and seedlings were now constantly raised.

Hence Gallesio concludes that much more was effected for the naturalization of the orange in Italy by the accidental production of new kinds from seeds during a period of about sixty years than had been effected by grafting old varieties during many ages.

It is hardly necessary to give other illustrations of this law, for no one with any knowledge of the subject will be inclined to question it. It is strange that its significance has been overlooked, but this is probably due to the failure of students of the subject to perceive that it

is possible to believe that the transmission of variability is the peculiar function of the male cell, and also to acknowledge that variation may occasionally occur without its influence.

Our theory that variation is caused by the transmission of gemmules, and that there is no especial arrangement for their transmission to buds or to unfertilized eggs, while there is a special adaptation which has been slowly evolved during the evolution of sex for transmitting them to fertilized eggs, gives us a simple explanation of the fact that while bud variation is perfectly possible, it is extremely rare as compared with the variability of sexual offspring.

Darwin has been led, through the study of variability, to a conclusion which is very much like the explanation which is here presented. He says (*Variation*, Vol. ii. p. 325) that "we may infer from the occurrence of bud variation that the affection of the female element through external conditions may induce variability, for a bud seems to be the analogue of an ovule. But the *male element is apparently much oftener affected by changed conditions, at least in a visible manner, than the female element or ovule.*"

Bud variation is much more frequent in cultivated plants than it is in wild ones. Very few instances have ever been observed in plants growing wild or under strictly natural conditions, and Darwin states that "bud variation is most common in plants which have been highly cultivated for a long time."

The adjustment between a cultivated organism and its artificial or unnatural environment must, in most cases, be less perfect than that which has been slowly established between a wild organism and its natural environment. We should, therefore, expect domesticated and

cultivated forms to be more prolific of gemmules than wild species. The fact that bud variation, like ordinary variation, is most common in cultivated forms, seems to show that the tendency to vary is excited in buds, as it is in fertilized ova, by the influence of gemmules which are thrown off by the cells of the body under new or unnatural conditions, and we can easily understand why it should be more frequent where gemmules are abundant than in a form with few gemmules, for the chance in favor of the accidental transmission of a gemmule to a growing or nascent bud will increase as the number of gemmules increases.

Changed Conditions do not act directly, but they cause Subsequent Generations to vary.

This strange and, as I hope to show, highly significant law has been noted by many observers, and a long list of illustrations might be quoted.

As Darwin points out, it is certainly a remarkable fact that changed conditions should at first produce, so far as we can see, absolutely no effect, but that they should subsequently cause the character of the species to change.

The late Dr. Jared P. Kirtland told me that for more than forty years he tried in vain to obtain varieties from the common red cherry, but that when at last varieties began to appear the variability was very great: that after it had once become established it continued for many years with no diminution.

It is well known that when new flowers are first introduced into gardens they do not vary, although all, with rarest exceptions, ultimately vary.

Darwin, in his *Variation,* Vol. ii. p. 316, quotes the following illustrations of this law: "Mr. Salter re-

marks that every one knows that the chief difficulty is in breaking through the original form and color of the species, and every one will be on the lookout for any natural sport, either from seed or branch; that being once obtained, however trifling the change may be, the result depends upon himself. M. de Jonghe, with reference to pears, says the more a type has entered into a state of variation, the greater is its tendency to continue doing so, and the more it is disposed to vary still further. Vilmore says that when any particular variation is desired the first step is to get the plant to vary in any manner whatever, and to go on selecting the most variable individuals, even though they vary in the wrong direction; for the fixed character of the species once broken, the desired variation will sooner or later appear.

Darwin gives quite a list of authorities to show that after English dogs have been bred for a few generations in India they degenerate, not only in their mental faculties, but in form.

According to Bachman, turkeys reared from the eggs of wild ones lose their metallic tints and become spotted with white in the third generation.

It will be seen from the instances which have been given that the number of generations which are exposed to the new conditions before variation is induced varies greatly. In the case given by Dr. Kirtland, fifty years elapsed before variations of the red cherry began to appear. In the case last quoted, variation appeared in the third generation, and Yarrell says that Australian dingos bred in the Zoological Gardens of England, almost invariably produced in the first generation puppies marked with white and other colors.

Sir Charles Lyell mentions that some Englishmen en-

gaged in conducting the operations of the Real del Monte Company in Mexico, carried out with them some greyhounds of the best breed to hunt the hares which abound in that country. It was found that the greyhounds could not support the fatigues of a long chase in this attenuated atmosphere, and before they could come up with their prey they lay down gasping for breath; but these same animals have produced whelps, which have grown up, and are not in the least degree incommoded by the want of density of the air, but run down the hares with as much ease as do the fleetest of their race in this country.

It is interesting to note in this connection that a tendency to vary is strongly inherited independently of the inheritance of any particular variation. Darwin believes that this tendency to vary may be transmitted by either parent, and he says (*Variation*, ii. 325) it is certain that variability may be transmitted through either sexual element, whether or not originally excited in them, for Kölreuter and Gärtner found that when two species were crossed, if either one was variable the offspring were rendered variable.

We have already pointed out that the crossing of species is in itself one of the most efficient causes of variation, and we can hardly base upon the observations above given the conclusion that variability may be transmitted by either sex.

The fact that changed conditions do not directly produce variation, but cause subsequent generations to vary, is precisely what we should expect, according to our theory: for a change in the environment of an animal or plant must disturb the harmonious adjustment which natural selection has brought about between the cells of its body and their conditions of life. Such a

change, if considerable, could hardly fail to affect certain cells unfavorably; and it would therefore cause the production of gemmules, thus inducing variation in later generations.

We can also understand how a tendency to vary may be hereditary, for if certain cells of the body vary, they will exercise a disturbing effect upon adjacent or related cells, and these, transmitting gemmules, will hand on the tendency to vary to succeeding generations.

Secondary Laws of Variation.

The law that variability is itself hereditary involves a number of secondary laws, all of which find a ready explanation in our theory of heredity.

Among these secondary laws is the law that "*specific characters are more variable than generic characters.*" Darwin has given the evidence of the existence of this law ("Origin of Species," p. 122), so it will not be necessary to discuss it, or to do more than point out that the theory of heredity furnishes an explanation of it.

The characters which are common to all the species of a genus, and which distinguish it from other genera, are, as a rule, much older than those which distinguish one species of the genus from the other species. The specific characters or features which distinguish each species of a genus from the others, are features which have appeared as new variations since the time when the various species diverged from the common ancestor from whom they inherit their common or generic characters. As specific characters are of more recent acquisition than generic characters, natural selection will have had less time to act upon the former than upon the latter. The adjustment between a specific character and its environment will therefore be, as a rule, less complete and per-

fect, and the cells which are involved will therefore have a greater tendency than those involved in generic characters to throw off gemmules. These characters will therefore be more variable in the descendants than generic characters.

Another law, the evidence for which is given by Darwin on page 44 of the "Origin of Species," is that "*species of the larger genera in each country vary more frequently than the species of the smaller genera.*"

When a country contains a great number of species of a genus it is generally safe to conclude that they have recently varied and diverged from each other. As the tendency to vary is in itself hereditary, and as one variation is in itself a cause of other variations, our theory of heredity would lead us to expect species which have recently undergone considerable change to show a tendency to vary still further, and we should therefore expect the species of large genera to be, as a rule, more variable than the species of small genera, although there is no reason why this rule should be absolute.

A still more interesting law is that "*a part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable*" ("Origin of Species," p. 119).

When one species of a genus agrees with the other species in most particulars, but differs from them all in some one respect, we may conclude that the peculiar organ or feature has recently been modified. Natural selection has therefore had less time to perfect the adjustment between this part and the remainder of the body than it has had to perfect the relations between other parts, or between the same parts in the other species.

This peculiar part will accordingly be in a favorable state for the production of gemmules, and it will there-

fore be more likely than a part which has not recently varied to vary still farther.

Walsh has called attention ("Proc. Entomolog. Soc.," Philadelphia, October, 1863, p. 213) to what he calls the "Law of Equable Variation," which is, "*if any given character is very variable in one species of a group, it will tend to be variable in allied species, and if any given character is perfectly constant in one species of a group, it will tend to be constant in allied species.*"

This is by no means an absolute law, but simply a general rule. Darwin points out that something of the same kind occurs in domesticated races, and that in the forms which are now undergoing rapid improvement those parts or characters which are most valued vary the most.

We can readily see that circumstances which cause a certain part to throw off gemmules, and thus induce variability, in one species, will be likely to produce the same effect on allied species living under similar circumstances. We can also understand that the divergent modification which has resulted in the formation of several species or races from a parent form, will in itself be a cause of still further modification in the same general direction.

Another well-known law, of which many examples will be given in Chapter IX. is that secondary sexual characters are highly variable. In the chapter on this subject I shall show that the distinctive sexual characters of a species are usually due to recent modification. Their great variability is therefore due to the same cause as that which renders specific characters more variable than generic, and is exactly what our theory would lead us to expect.

Natural Selection cannot produce Race Modification unless the Same Part tends to vary in a Number of Individuals at the Same Time.

This argument, which seems to me to be the most important one which has ever been adduced against the theory of natural selection, was first advanced by a writer in the *North British Review* in June, 1876.

The author points out that since the chance of survival of any particular individual which is born is very slight indeed, the birth of an individual with any particular slight advantage, and its consequent superiority over its fellows, would not be sufficient to over-balance the chance of its destruction. The objection, which is purely logical, and not experimental, will be stated at length in another place. At present the fact that those who are best qualified to judge, Darwin among them, have acknowledged its great weight, will suffice to show that it is a real and valid objection, and that the foothold of the theory of natural selection would be greatly strengthened if we could show that the causes which produce variation act in such a way as to cause the same part to vary at the same time in great numbers of individuals.

According to our theory of heredity, this will generally be the case. We suppose that an unfavorable change in the environment of a particular cell causes this cell to throw off gemmules. It is plain that a change in the external world, which unfavorably affects any particular cell or group of cells in one individual, will usually affect the corresponding cells of other individuals of the species at the same time. When any particular cell is prolific of gemmules in one individual of a species, the same thing will usually be true of the same cell in other

individuals, and the corresponding cell will therefore be a hybrid, and will tend to vary in many descendants.

In each of these descendants this hybrid will be composed of almost identical elements, and they will all tend to vary in the same or nearly the same manner; and as each variation causes other cells to throw off gemmules, the number of individuals which are similarly modified will tend to increase from generation to generation, and natural selection will therefore act, not on a single exceptional individual, but upon a great number, all of which are modified in essentially the same way.

If Variation is Purely Fortuitous, the Evolution of a Complicated Organ composed of Many Parts by Natural Selection demands a Period of Time which is almost Infinite.

This obvious objection to the law of natural selection has been so frequently discussed that it is unnecessary to dwell upon it at present, especially as I shall examine it in detail in another place. At present I will only call attention to the fact that a variation in any part of a complicated organ will, in itself, disturb the harmonious adjustment of other parts, and will thus cause them to throw off gemmules, and thus to induce variability in the next generation.

The fact that change is needed in any part will be the cause of variation in this part, and the time which is needed to restore all parts of an organ to a position of equilibrium will thus be almost infinitely reduced. The argument of those who hold that life has not existed upon the earth long enough for the evolution of all the adaptations of nature by the selection of fortuitous variations will thus lose all its weight.

Saltatory Evolution.

Darwin believes that the evolution of wild species is due, like the formation of many domesticated races, to very slow modification by the natural selection of great numbers of very slight and inconspicuous variations, but many other authors have given reasons for believing that this is not the case.

Many of our most peculiar domestic races have originated suddenly, and there are reasons for believing that the history of the evolution of each species is divided into periods of abrupt and extensive modification, alternating with periods of comparative stability. This subject, like those which have been briefly noted in the last two sections, will be fully discussed in Chapter XI., and I will only dwell upon it long enough at present to point out that our view of the cause of variation implies that any particular change should in itself be a fruitful source of still greater modification, so that as soon as a tendency to vary becomes established it will continue to increase until an equilibrium is again established by the natural selection of those modifications which are adapted to the environment.

Correlated Variation.

This subject will be fully discussed in the chapter on homology, but a few words upon it will not be out of place here.

Darwin, who frequently uses the term, includes under it facts which belong to two somewhat different classes. When any part varies, the organs with which it is most directly associated also tend to vary in such a way as to restore the harmonious adjustment between the various parts: and a variation in one part is often accompanied by variation in homologous parts.

These two cases shade into each other somewhat, but it will be convenient to treat them separately. The first has just been briefly examined, p. 156, and what follows relates only to the second class of cases—the variation of homologous parts.

The most familiar illustration of this law is the fact that in most bilateral organisms homologous parts on both sides of the body tend to vary together. The law holds in radially symmetrical organisms also. All the petals of a regular flower generally vary in the same manner, but there are many exceptions.

The front and hind limbs of vertebrates tend to vary in the same manner, as we see in long and short legged or in thick and thin legged races of horses and dogs.

It is stated that when the muscles of the arm depart in number or arrangement from the proper type they almost always imitate those of the leg, and so conversely the varying muscles of the leg imitate the normal muscles of the arm. There are many cases where a parent with extra fingers has produced a child with extra toes, or the reverse, and in other cases a parent with only one extra digit on one hand has had children with supernumerary digits on both hands and both feet.

In certain pigeons and fowls, especially in the trumpeter pigeon, long feathers, like the primary wing feathers, grow on the outside of the leg and on the two outer toes, and in pigeons with the feet thus feathered the two outer toes are partially connected by skin, thus showing a marked anatomical resemblance to a wing.

The various appendages which are formed from the skin, such as hoofs, horns, hair, feathers, teeth, etc., are homologous organs, and it is interesting to notice how frequently a peculiarity in one of these structures is associated with similar peculiarities in others.

Tropical sheep with long coarse hair usually have goat-like horns. Inherited baldness in man is often accompanied by deficient teeth, and the renewal of the hair in old age by a renewal of the teeth. The famous hairy Burmese had deficient teeth, and both peculiarities were hereditary. A Spanish dancer, Julia Pastrana, had a full beard and a double set of teeth, and the daily papers have recently contained an account of a man, living near Lebanon, Pennsylvania, with no hair, teeth, or sweat glands.

The homologous parts of plants often vary in the same way, as is well shown by certain compound flowers, in which the stamens and pistils closely resemble petals.

According to our view of the cause of variation we can easily see how gemmules from a cell in one hand might hybridize, and thus cause variation in the corresponding cells of all four extremities, or perhaps in the embryonic cell from which all these cells are derived, for in the same way that an animal can unite sexually either with another of its own race or with one which is somewhat less closely related to it, so I assume that a gemmule may unite with the particle of the ovum which corresponds to it, or with some other closely related particle. For example, a gemmule which is thrown off from a particular epithelial cell may simply cause modification in the corresponding cell of the offspring, or it may cause modification in a cell which is to produce this particular cell and a number of others.

If each variation is purely fortuitous the number of generations which would be necessary in order to convert a species with black hair into a species with every hair brown or with every hair red is almost inconceivable, but this difficulty entirely disappears as soon as we recognize that gemmules from one part of the parent may

affect all the homologous parts of the offspring in the same way and at the same time.

Males more Variable than Females.

One of the most remarkable and suggestive of the laws of variation is that in all the higher animals a part which is confined to males, or is more developed or of more functional importance in males than it is in females, is very much more variable than a part which is confined to females or is more important in females than it is in males.

The evidence for this remarkable law will be presented at length in Chapters VIII. and IX. The existence of such a law is absolutely inexplicable without the theory of heredity, but it is exactly what this theory would lead us to expect, for an organ which is most important in one sex is most likely to be influenced in this sex by changed conditions, and is therefore more likely to form gemmules in the body of the sex where it is most important than in the body of the opposite sex. An organ which is most important in males will therefore be most prolific of gemmules in males, while an organ which is most important in females will be most prolific of gemmules in females. Gemmules which are formed in the male body are vastly more likely to be transmitted to descendants than those which are formed in the female body. It follows that an organ which is most developed or most important in males must be vastly more likely to transmit gemmules to descendants, and therefore to vary in successive generations than an organ which is most developed or most important in females.

Another law which follows from the one which has just been stated is that males are as a rule more variable than females. This law has been noticed by Darwin and others, but no explanation has ever been advanced.

Summary of Last Two Chapters.

The study of hybrids and of variation has led to the discovery of a great number of general laws, all of which are perfectly explicable by the theory of heredity, and are precisely what it would lead us to look for, although most of them are absolutely inexplicable without it, and have no place in any other hypothesis which has ever been proposed to account for the phenomena of heredity.

The study of hybrids gives us a means of analyzing to a certain extent the influence of each sex in heredity, but our experiments in this direction are limited by the fact that organisms must be very closely related in order to breed together, and parents which are very closely related must be essentially alike in everything except the most recently acquired modifications. So far as they enable us to analyze the influences of the sexes, the results furnished by hybrids agree with the demands of our theory. This furnishes an explanation of the great variability of hybrids, as compared with the pure parents, and it also enables us to understand why hybrids from domestic races should be more variable than those from wild races.

The remarkable fact that the descendants of hybrids are more variable than the hybrids themselves receives a simple explanation by our assumption that exposure of the various cells of the body to unnatural conditions is the prime cause of variability, and that it acts indirectly by causing the production of gemmules.

Some of the recorded facts regarding hybrids are so very peculiar that it would be difficult to devise better tests than they furnish of the truth of our theory. What could be more curious or more opposed to the

view that the sexes play similar parts in heredity than the fact that the offspring of a male hybrid and the female of a pure species is much more variable than the offspring of a female hybrid by a father of pure blood? Darwin's pangenesis hypothesis furnishes no explanation of this most remarkable fact, and none of the hypotheses of heredity which have been proposed from time to time are sufficiently definite to have any bearing upon a concrete case like this, but our theory that changed conditions of life cause a production of gemmules, and that these are stored up in and transmitted by the male element, fits this case exactly.

The curious phenomena of reciprocal crosses, again, are just what our theory would lead us to expect, and it also furnishes us with an explanation of the fact that crossing so frequently causes reversion.

A comparison of sexual with asexual reproduction also gives us a means of analyzing the influences of the two sexual elements, for asexual reproduction is essentially reproduction with the male element left out, and the result of this omission is, as we should expect, the reduction of the tendency to vary to a minimum. At the same time that our theory explains the great rarity of bud variations, it admits of their occasional appearance, and it gives an explanation of the singular fact that bud variation is much less rare in plants which have long been cultivated than it is in wild forms.

The most remarkable of the laws of variation is the well-known law that changed conditions do not directly produce variation, but cause subsequent generations to vary. As changed conditions do not in themselves cause hereditary modification, but simply lead to the production of gemmules, we see why their effect should be manifested in succeeding generations, and we also see

why variation is itself hereditary, for the variation of any particular cell will cause adjacent or related cells to throw off gemmules, and thus to produce variation in successive generations.

We can also understand why specific characters should be more variable than generic characters; why the species of large genera should vary more than the species of small genera; why a part developed in an unusual way or to an unusual degree should show a marked tendency to vary, and why secondary sexual characters should exhibit a similar tendency.

Unless our theory is true, what possible reason can there be why a part which is excessively developed in males should vary more than a part which is similarly developed in females alone, or why the males of our higher domesticated animals should be more variable than the females? Its power to deal with and interpret special cases of this kind separates our theory from all other attempts to explain the phenomena, and seems to show that there can be but one choice between it and any other explanation which has ever been proposed.

If we accept Darwin's view that variations are purely fortuitous, there are certain grave difficulties which must prevent us from giving the theory of natural selection unqualified acceptance as an adequate and complete explanation of the origin of species.

Natural selection can rarely lead to permanent modification unless many individuals tend to vary in nearly the same way at about the same time, and if variation is fortuitous the chance against this is very great indeed. While there is no reason to doubt that natural selection might bring about all the changes which have led to the formation of a complicated organ, by the preservation of fortuitous variations, if time enough were given, there is

reason to doubt whether life has existed long enough to permit the evolution of existing forms in this way, and natural selection gives no account of the sudden appearance of considerable modifications, although the history of domestic animals shows us that such saltations do sometimes occur.

On the one hand we find that Darwin's assumption that variations are fortuitous involves us in grave difficulties, but on the other hand we find scarcely any evidence to show that permanent hereditary race modifications are ever directly produced by the action of external conditions, while we do find evidence for the opinion that race modifications are, as a rule, not due to this direct action, but to congenital variation.

Our theory furnishes an explanation which lies midway between Darwin's view of the origin of variation and the Lamarkian view, and thus enables us to escape both these difficulties, for it shows us how the influence of changed conditions upon an organism may give rise to congenital variation in later generations, and it also shows us why variations tend to appear at the time and place where they are needed. It also shows how a considerable modification may appear suddenly and become hereditary.

The correlated variation of homologous organs and the correlated modification of the various parts of a complicated organ are accepted by Darwin without explanation, but the theory of heredity shows us that these phenomena, the chance against the fortuitous occurrence of which is almost infinite, are due to the working of a very simple law.

When we review the ground and see how all the phenomena of hybridization and variation fall into their proper places; how the same simple explanation fits the

most anomalous and exceptional phenomena as well as the more ordinary and simple cases, I think we must acknowledge that our theory is at least an approximation to the truth.

If it leads us to the discovery of truth, and thus ultimately contributes to the establishment of an explanation of the phenomena of heredity, its final acceptance in its present form is a matter of little moment. That it is a great advance beyond all the attempts which have been recorded seems obvious, and an examination of the ground which it covers certainly seems to show that it is a step in the right direction.

CHAPTER VIII.

THE EVIDENCE FROM SECONDARY SEXUAL CHARACTERS.

The Nature of this Sort of Evidence.

I HAVE already given many reasons for believing that the male reproductive organ is especially adapted for gathering up the gemmules which are thrown off by the cells of the body; and for transmitting them to the next generation by impregnation, thus giving rise to variation; while the transmission of the gemmules which are formed in the body of the female is not thus provided for.

If this supposition is correct, we should expect to find that a variation which first appears in a male should have more tendency to become hereditary than one which first appears in a female. Any slight change in either the male or the female body will, as we have already seen, cause all the cells which are either directly or indirectly influenced by the change to throw off gemmules. This will happen in a female body as well as in a male body, but the gemmules are, in the latter case, much more likely to be transmitted to descendants, and thus to give rise to more extended modification.

We should also expect to find that an organ which is confined to males is much more likely than one which is confined to females to undergo hereditary changes, for even if the parts of the female body give rise to gemmules as frequently as the parts of the male body, the chance of transmission is much less.

We should also expect to find that parts which are

confined to males are more variable than parts confined to females; for variation in any part is due to inheritance of a gemmule from the corresponding part of one parent or the other, but when the part is found in only one parent the gemmule must come from that parent.

As transmission of gemmules by the mother is more rare than transmission by the father, it is plain that parts which are confined to the male should be expected to vary more than parts found in the female alone.

Finally we should expect the male body as a whole to be more variable than the female body, for the same reason.

In most cases it is impossible to trace any particular variation back to its first appearance. This is almost out of the question with wild animals, and most domesticated races have been formed so slowly that it is impossible to say whether the successive steps appeared in males or in females, nor can we be sure that a variation is new when it first attracts attention. Still it is interesting to note that the sudden variation which resulted in the ancon breed of sheep was first noticed in a male, although it is, of course, impossible to say whether it was due to inheritance of gemmules from the father rather than from the mother. Certain hereditary diseases and montrosities, such as albinism or polydactylism, are fully as often traceable to a male origin as they are to a female origin, but as we know that peculiarities of this kind frequently skip a generation or two, we can never be sure that we have traced them to their origin.

In the secondary sexual characters of animals we have a class of phenomena which are not rare and exceptional, for they are numbered by hundreds of thousands, and they can be observed and studied by every one.

A secondary sexual character is a peculiarity which is not directly concerned in the reproductive process, although it is normally either confined to one sex, or else is much more developed in one sex than it is in the other. The presence of a beard is a secondary sexual character of man; the comb, wattles, spurs and brilliant plumage of the domestic cock, the horns of a stag, the tusks of an elephant, the mane of a lion, or the brilliant plumage of the peacock or of the drake, are all of them examples of this sort of organs, for they are either confined to one sex, or else they are much more conspicuous and important in one sex than they are in the other.

They furnish, like hybrids, a means of disentangling or analyzing to some extent the influence of the two sexes in heredity, and I hope to show in this and the following chapters that they furnish evidence to prove—

1. That in most animals with separate sexes the males of allied species differ more than the females from the ancestral type.

2. That organs which are confined to males or are of more importance or are more perfectly developed in them than in the females, are much more likely to give rise to hereditary modifications than parts which are confined to or are most developed in females.

3. That a part which is confined to or is most developed in males is more likely than a similar female part to vary.

4. That males are, as a rule, more variable than females.

5. That the male leads and the female follows in the evolution of new races.

There are two criteria which are of great use in the attempt to trace the path which a species has followed in its evolution. One of these is by comparison of a

species with its nearest allies. The other is by comparison of the young with the adult.

If most of the species of a genus resemble each other in certain characters, while one species presents a marked deviation, we may in most cases safely conclude that the latter species has undergone recent modification in this respect. Of course this rule does not hold good where the peculiarities of the exceptional species are features of resemblance to other genera of the family, for in this case we must conclude that it has remained comparatively stationary, while all the other species of the genus have been modified.

If in the second place we find that the adults of several related species differ greatly, while the young are much alike, we must attribute the difference in the adults to the fact that they have recently diverged from a common stock.

Now I hope to show that throughout the animal kingdom, wherever the sexes differ from each other, the general law holds good that the males of allied species differ from each other more than the females do, and that the adult male differs more than the adult female from the young. There are many marked exceptions to this law, but the existence of the law has long been recognized by all naturalists. Every one who has worked at the systematic zoology of insects or vertebrates knows how difficult it often is to decide upon the specific identity of an immature or a female specimen, even in cases where the mature males can be recognized and identified without difficulty.

Darwin's interesting essay on "Sexual Selection" is well known. It is almost entirely devoted to the study of secondary sexual characters, and to a masterly discussion of the subject in all its aspects and relations.

Darwin has gone over the whole field so thoroughly and exhaustively that little remains to be said upon the subject, and the reader who is familiar with the essay will discover that almost all the facts in this chapter are borrowed from this source.

Darwin's aim, however, is simply to show the potency of sexual selection, while our present object is to show the frequency of hereditary male modification as compared with female modifications, and I have therefore rearranged the facts, so as to give especial prominence to this aspect of the subject. The critical reader will discover that in many cases I have borrowed the descriptive portion of one of Darwin's paragraphs, but have said nothing about the theoretical portion. As Darwin's conclusions are in many cases opposed to my own, this may convey to some the impression that I have made an unfair use of the weight of his authority, and have quoted him in support of conclusions which he in reality opposes. I will refer such readers to the chapter which follows this, where I have devoted a section to a statement of Darwin's view of the origin of secondary sexual characters, and have given my reasons for believing that it is only a partial explanation of the phenomena in question.

Examples from Various Groups of the Animal Kingdom to show that in all Groups where the Sexes are Separate the Male is, as a Rule, more Modified than the Female, and that the Adult Males of Allied Species differ more, as a Rule, than the Females or Young.

Rotifera.—In 1849, Dalrymple (Description of an Infusory Animalcule allied to the Genus Notommata, *Phil. Trans.* 1849) made the interesting and remarkable discovery that, in one species of the Rotifera, *Notom-*

mata Anglica, the animals are not hermaphrodites, as earlier writers had supposed, but that the males, which are rarely met with, are very much smaller than the females. The latter sex is furnished with a digestive tract which is quite complicated in structure, and is armed at the mouth with a highly specialized masticating apparatus. The digestive organs of the male, on the other hand, are almost absent. The jaws, the œsophagus and the mouth are wanting, and the stomach and intestine are reduced to a functionless rudiment. The males receive no nourishment after they leave the egg, and they live only a short time. The presence of a digestive tract is characteristic of all groups of animals above the protozoa, so we are compelled to believe that the ancestral form from which the Rotifera are descended had, like the ordinary metazoa, a mouth, a stomach, and an intestine; and no one who is at all familiar with comparative anatomy can doubt that the male, in which it is absent, rather than the female, in which it is present, is the sex which has been modified. The digestive tract is usually one of the first parts to be developed in the embryo, and its disappearance or absence in the adult male rotifer is therefore very different from the absence of the wings in certain female insects. Wings appear very late in life, and the failure of the female to acquire them is simply an arrest short of perfect development, while the absence of digestive organs shows active degeneration. In 1855 Leydig verified Dalrymple's observation (*Zeit. f. Wiss. Zool.* vi. p. 96) in the same species, and also in a second species of the same genus; and as he was able to distinguish the outline of the male inside the egg, while this was still contained within the body of the female, he removed all reason for doubting that the two sexes belong to one

species. In these two species the females were much alike, while the males were not only very different from the females, but also from each other.

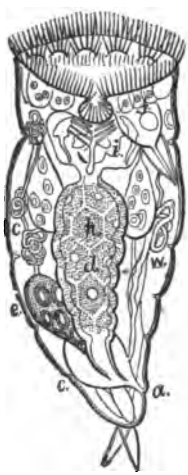


FIG. 1. Young female Rotifer. *Hydatina senta.* *a.* cloaca. *b.* contractile vesicle. *c.* water tubes. *d.* stomach. *e.* ovary. *f.* ganglia. *g.* stomach. *i.* mouth-parts.

FIG. 2. Male of the same species. *a.* orifice of penis. *b.* contractile vesicle. *c.* testes. *d.* ganglion. *e.* setigerous apparatus.

Since the year 1855 the subject has been studied by many naturalists, and the males have been found in such a number of species that it is probable that the

sexes are separate in all the Rotifera. In some forms the males are even more simplified than in *Notommata*, while in others they are less so, and in a few they are like the females in size and structure, and have the digestive organs perfectly developed.

ANNELIDS.—Among the marine polychætous annelids there is often considerable difference between the sexes, and the points in which the male differs from the female are also points in which the males of various species differ from each other.

ARTHROPODA.—Among the Arthropods, the Insects, Crustacea, etc., the female is often very greatly modified, and in some cases the females of allied species differ from each other much more than the males, and in other cases it is hardly possible to say whether the males or the females of allied species differ most, but, taking the group as a whole, the Anthropods seem to follow the law which prevails in other groups of animals, and male modifications are more numerous than female modifications.

In the Branchiopod Crustacea the males are smaller than the females, and are much less abundant. The male differs from the female in the possession of a number of secondary sexual characters. The second antennæ of the male are more richly supplied with sensory hairs than those of the female, and various appendages of the male may be so modified as to form clasping organs for holding the female. In Branchippus the second antennæ of the male are greatly modified for this purpose. Figure 3 shows the head of a female specimen of *Branchippus Grubei*, figure 4 the head of the male of the same species, and figures 5 and 6 the heads of the males in two closely allied species. These figures show how much the males of the various species

differ from each other in this respect. The shape and structure of the first antennæ and of the abdomen may

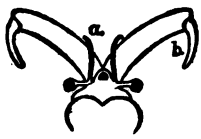


Fig. 3. Head of female specimen of *Branchippus Grubei*, greatly enlarged. *a.* first antennæ. *b.* second antennæ.

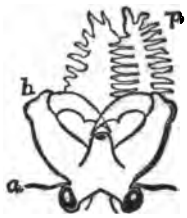


Fig. 4. Head of the male of the same species.

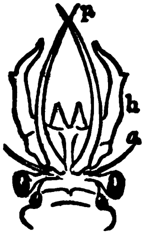


Fig. 5. Head of male *Branchippus stagnalis.*

Fig. 6. Head of male *Artemia salina.*

also show considerable modification in the males of various species of Branchiopods.

Among the Cladocera, of which the common *water-flea* of our fresh-water ponds and lakes is an example, the female is provided with a brood pouch, within which the eggs are carried and the young developed. In the male these structures are absent, and the second antennæ are especially modified as organs for discovering and holding the female. They are richly supplied with sensory hairs, and they are often armed at their tips with grappling hooks, which differ in the males of closely allied species.

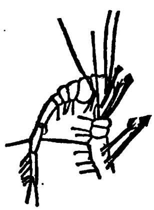


FIG. 7. Antenna of male *Cyclops serrulatus.*

FIG. 8. Antenna of male *Cyclops canthocarpoides.*

The Ostracoda present sexual differences like those in the Cladocera, and in many of them it is certain that the male part deviates, more than the female part, from the typical form.

In the non-parasitic Copepods, of which the fresh-water *Cyclops* (Fig. 9) is an example, there is not very much difference between the sexes, although certain appendages, which are unmodified in the female and retain their typical form, sometimes differ greatly in the males of allied species, and may be specially mod-

ified for discovering or holding the female. The modification of the first antenna of the male for this purpose is quite general, and a comparison of this part in the males of various species of Cyclops (Figs. 7 and 8) with the same part in a female (Fig. 9), shows how much the males of allied species differ in this respect. The second antennæ, the maxillary feet, and the last pair of

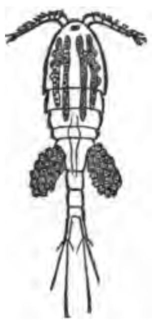


FIG. 9. Female specimen of *Cyclops canthocarpoides.*

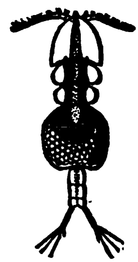


FIG. 10. Female specimen of *Notodelphys Allmani.*

swimming feet, are sometimes modified in the same way in the male. In the male Saphirrina the wonderful display of brilliant colors is due to the presence of peculiar color-producing organs, which are absent in the female.

Among the parasitic Copepods we find a departure from the ordinary typical structure, which is so remark-

able that no one, on first examining one of the more modified parasitic forms, such as the one shown in Fig. 15, would detect any resemblance to the free or non-parasitic members of the group, or would even suspect that the animals are crustaceans.

The females, which are known as "*fish-lice*," are parasites upon fishes and other aquatic animals, while the males are parasites upon the bodies of the females, and are usually of minute size as compared with the females.

The adaptation to a parasitic life has not only produced the most profound changes in the general structure, but it has also brought about an almost unparalleled difference between the sexes. It is true that this is not due to the modification of males alone, for the females as well as the males exhibit the most extreme departures from the organization which is characteristic of typical or non-parasitic crustacea, and it is difficult to decide from structure alone whether the male or the female is most modified. The fact that the male has been adapted to a life as a parasite upon the body of the female, while the female has simply become adapted to a parasitic life on other animals, seem to show that the male organism is somewhat more plastic than the female. Simple parasitism may be brought about by indefinite variability, but parasitism upon a parasite demands definite variation to meet the definite changes which have taken place in the host.

The highly specialized parasitic Copepods are joined to the non-parasitic forms by a long series of intermediate species, in which the parasitic habit is only slightly developed, and I give a few figures to illustrate some of the steps in this most interesting series. The female *Notodelphys* (Fig. 10), which lives in the body cavities

of marine invertebrates, and has very limited powers of locomotion, hardly differs from the non-parasitic Cyclops (Fig. 9), except that two of the body segments are modified to form a chamber in which the eggs undergo their development. The male (Fig. 11) is somewhat

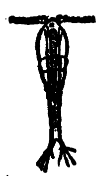


FIG. 11. Male specimen of the same species.

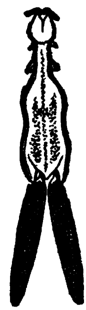


FIG. 12. Female specimen of *Lernentoma corunta*.

smaller than the female, but bears a close resembance to her, and to ordinary copepods.

The female *Lernentoma* (Fig. 12) is very different from the male (Fig. 13), and both depart very greatly from the typical copepod structure, although a slight resemblance can be traced between the female and cyclops. The female is very much larger than the ordi-

nary non-parasitic forms; the segmentation of the body is hardly visible, the power of locomotion is entirely lost, and the appendages are either rudimentary or are changed into hooks for clinging to the animal infested by the parasite. The male, like the female, has no power of locomotion, and is very much smaller than the female, the difference in size being much greater than the two figures would indicate. It is found nowhere except upon the body of the female, to which it clings by its rudimentary feet. The female of another form, *Anchorella*, is shown in Fig. 15, and the male in Fig.

FIG. 13. Male specimen of *Lernentoma corunta.*

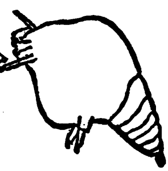


FIG. 14. Male specimen of *Anchorella uncinata.*

14. In this species the males are very small as compared with the females, to whose bodies they are firmly fastened by their rudimentary hooked limbs.

We can hardly state with confidence that either sex is more modified than the other in these parasitic copepods, for both have undergone such great changes that they have lost all traces of their crustacean affinity, but in the very similar case of the barnacles, we have sufficient evidence that the males do depart further than the females from the ancestral type.

The barnacles, or acorn-shells (Fig. 16), are crustacea

which are pretty closely related to the copepods, which they resemble somewhat, during the early stages of their development. The young swim freely in the water for a time, but finally attach themselves to foreign bodies, head downwards, by their antennæ, and are sedentary for the rest of their life. In the stalked or pedunculated barnacles, the antennæ of the free larva become replaced in the adult by a long peduncle, at the top of

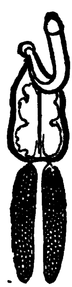


FIG. 15. Female specimen of *Anchorella uncinata.*

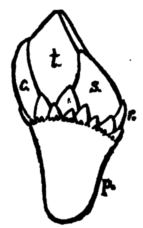


FIG. 16. An hermaphrodite stalked barnacle. *Pollicipes cornucopia.* *c.* carina. *t.* tergum. *s.* scutum. *r.* rostrum. *p.* peduncle.

which there is an irregularly triangular box, the capitulum, made up of a number of calcareous plates. Inside this box the animal is placed, head downwards, and although it is greatly modified to fit it for this protected sedentary life, it still presents unmistakable evidences of its crustacean affinity, such as the mouth-parts, the segmented body and limbs.

One of the most remarkable characteristics of the Barnacles is that, with a few exceptions, they are hermaphrodite. The Arthropoda include a very considerable proportion of all the animals which are known to us, and as all of them, except the Barnacles and a few closely related parasitic forms, have the sexes separated, the fact that these few sedentary forms are hermaphrodite is certainly very remarkable, and we must believe that they are the descendants of crustacea with separate sexes. The stalked barnacles resemble typical crustacea much more closely than do the sessile ones, and we must regard the former as more closely related than the latter to the ancestral form with separated sexes. It is, therefore, interesting to find that a few species of stalked barnacles are male and female, and also that in a few others the ordinary hermaphrodite form is accompanied by a parasitic male, which has been called by its discoverer, Darwin, a complementary male.

The study of the few species with separate sexes and of those with complemental males has brought to light some of the most remarkable phenomena of natural science, and the subject is well worthy of extended notice.

Figure 16 is an ordinary hermaphrodite stalked barnacle, *Pollicipes.* It belongs to a genus in which no true males or true females are ever found.

Figure 17 is a species belonging to a closely related genus, *Scalpellum,* and it will be seen at once that it closely resembles *Pollicipes,* even in the arrangement of the plates of the capitulum. It is an hermaphrodite-like *Pollicipes,* but with a difference, for it carries inside its shell a small parasitic complemental male, which is shown in Fig. 18. This male is very much smaller than the hermaphrodite, and Fig. 17 is considerably magni-

fied, while Fig. 18 is of nearly the natural size; but with this exception the complementary male is essentially like the hermaphrodite, and it has the structure of an ordinary stalked barnacle. There is a distinct peduncle, which carries a triangular capitulum, and although the plates are somewhat reduced in number they agree in form and position with the chief plates of such a species as *Pollicipes.* The animal inside the capitulum is much like an ordinary barnacle, the essential difference being the total absence of female reproductive organs. It is a male and nothing more.

FIG. 17. An hermaphrodite barnacle. *Scalpellum villosum.*

FIG. 18. Complemental male of the same species.

Figure 19 shows the female of another species, Ibla *Cummingi,* which does not differ essentially from the forms shown in Figs. 16 and 17, but the female of *Ibla Cummingi* is a true female instead of an hermaphrodite, and there are no traces of male reproductive organs, but inside her shell, and planted by a long root-like process, there is a minute parasitic male, shown in Fig. 20, magnified thirty-two times, while the figure of the female is magnified only five times. In Fig. 20, *b* is part of the wall of the body of the female, and *a* is the long root by which the parasitic male is planted.

The male has a capitulum, but no calcareous plates, and its antennæ, an., are not completely merged in the peduncle. It also differs from the female in the possession of an ocellus, or eye-spot· It has mouth-parts and limbs, and, except for the fact that all its parts are somewhat rudimentary, it does not differ very greatly from other barnacles, except as regards its reproductive organs.

In other species of Scalpellum, however, as in Scal-

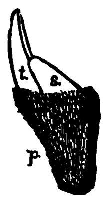


Fig. 19. Female specimen of *Ibla Cumingii.*

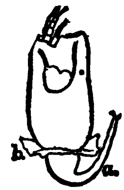


Fig. 20. Parasitic male of the same species.

pellum Regium, the male is still more rudimentary, and has no mouth or digestive organs.

In two other genera, Alcippe (Fig. 21) and Cryptophyalus, the females, which are true females, with no trace of male reproductive organs, differ very essentially from ordinary barnacles, and they have fastened to the outside of their bodies a number of very small males. In the males of these two species, which are shown greatly magnified at Fig. 22, there are a few faint traces of muscular fibres, but the organs of digestion

are entirely gone, and the inside of the body is entirely filled with a great testis, while the posterior end is prolonged into an enormous penis; and the animal hardly deserves to be called an animal at all, as it is scarcely more than an independent male reproductive organ attached to the body of the female.

This is certainly one of the most remarkable cases of difference between the sexes, and no one who compares Figs. 18 and 22 with Figs. 16, 17 and 19, can doubt that

Fig. 21. Female of *Alcippe lampas.*

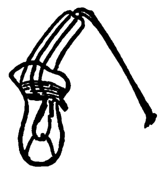


Fig. 22. Male of the same species.

among these barnacles the males differ from each other much more than the females.

Among the higher crustacea we find great numbers of cases where the young male is like the adult female, or the young of both sexes, but at maturity acquires distinctive sexual characters. Any one who is familiar with the crustacea will acknowledge the existence of this phenomenon, and it will only be necessary to give a few illustrations. The adult male Lucifer is distinguished from the adult female by the posses-

sion of a very peculiar clasping organ, figure 23, upon the first swimming appendage of the abdomen. The corresponding appendage, figure 24, of the adult female is like the other abdominal appendages of both sexes, and we must believe that the peculiar form, in the male, is due to recent modification. It is therefore interesting to note that, before the male reaches maturity, the limb in question is exactly like the other abdominal appendages of the adult male or adult female. The male Lucifer differs from the female in the shape of the last segment of the abdomen, and the outline of the

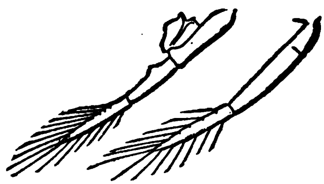


Fig. 23. First abdominal appendage of a male *Lucifer*. **Fig. 24. The corresponding appendage of the female.**

exopedite of the tail-fin is peculiar. These differences are very slight, as will be seen by comparing the terminal segments of the male, figure 25, with those of the female, figure 26, and it is hardly possible that they are of any direct service in reproduction. The fact that, in the young of both sexes, these parts are like those of the adult female, and that their peculiarities in the adult male are due to a final change which does not occur in the female, indicates that race-modification has gone a little further in the male Lucifer than it has in the female.

Darwin says that it seems to be a general rule among the crustacea, that the remarkable differences of structure which distinguish the male from the female, do not make their appearance until the male is nearly mature. In proof of this he refers to the fact that the male sand-hopper, does not acquire his large claspers, which are very differently constructed from those of the female, until nearly full grown, while the claspers of the young male resemble those of the female.

The history of the abdomen in crabs seems to show

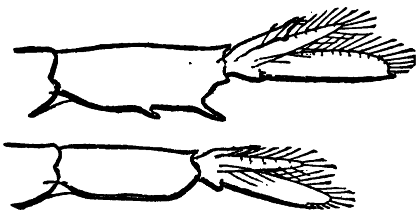


FIG. 25. Tip of abdomen of male *Lucifer*. FIG. 26. Tip of abdomen of female.

clearly that this difference is due to the fact that the male has deviated further than the female from the ancestral type. The long-tailed crustacea, like the cray-fish, have a long free movable abdomen, ending in an enlarged tail-fin, and composed of a number of segments, each of which carries a pair of appendages. In the female cray-fish the first of these appendages are like those behind, but in the male, the first ones are peculiarly modified and form copulatory organs. We have ample evidence that the true crabs are the modi-

fied descendants of an ancestral form which had, like the cray-fish, a long free tail, which was used in swimming. The fact that the young crab does have such an abdomen, is one of the proofs of the correctness of this view; but as the crab grows up, the abdomen becomes curled forwards under the body; it ceases to be used as a swimming organ; its separate rings become fused together, and its appendages become rudimentary or disappear. This very instructive change goes further in the male than it does in the female, for in the latter, more of the rings remain distinct; a greater number of appendages persist in the adult, and these are much more like those of the young, or of the cray-fish, than are those of the male.

The great modification of the male as compared with the female is well shown, among the crustacea, by the fact that there may be in the same species two different male forms. This *sexual dimorphism,* as it is called, is well shown in a Brazilian amphipod, *Orchestia Darwinii,* in which species there are two male forms which differ from each other in the structure of their large claws. These claws are used for holding the female, but as both forms are now used for this purpose, either shape would certainly have sufficed as well as the other, and this case therefore differs greatly from that of the social insects, where one form performs a certain duty in the community, while another form is adapted to fill a different place and perform a different duty. The two male forms in Orchestia seem to be due simply to the tendency of the male organism to become modified more rapidly than the female, and not to any great advantage which has resulted from the divergent modification. In discussing this case Darwin says that the two male forms have originated by some having varied

in one manner, and some in another: both forms having derived certain special but nearly equal advantages from their differently shaped organs.

Dr. Hagen has called attention to the fact that in certain of our American species of cray-fishes, there are two slightly different male forms, and Fritz Muller, who pointed out the existence of the two male forms of Orchestia, has also described a remarkable dimorphic species of Tanais, in which the male is represented by two distinct forms, never graduating into each other. In the one form the male is furnished with more numerous smelling threads, and in the other form with more powerful and more elongated claws to hold the female. Fritz Muller suggests that these differences between the two male forms of the same species must have originated in certain individuals having varied in the number of their smelling threads, while other individuals varied in the shape and size of their claws, so that of the former those which were best able to find the female, and of the latter those which were best able to hold her when found, have left the greatest number of progeny to inherit their respective advantages.

Whenever a number of species of a genus have any part more developed in the male than it is in the female, this part, as a rule, varies in the males of the different species, and is therefore of great systematic importance, since it furnishes diagnostic characters for distinguishing the species from each other. This rule is of general application, in all groups of animals with separate sexes, and every one who is at all familiar with the systematic zoology of our higher animals knows how difficult it is to identify species without mature male specimens.

The crustacea furnish an abundant supply of illustrations of this law, but we have space for only one.

In the fiddler crabs, one of the claws of the male is enormously developed, so that it compares with the other about as a base-viol does with its bow. In the female both claws are alike, and both small. There are a number of species of fiddler crabs, forming together the genus Gelassimus, and the big claw of the male, in each species, has certain points of difference from all the other species.

The fact that the features which characterize males as distinguished from females, are also the features which distinguish species from each other, certainly indicates that the origin of specific difference is to be sought in some peculiarity of the male organism.

INSECTS.—Many insects have stridulating organs, by which, as in the house-cricket, they produce their sharp music. In many cases these organs are exclusively confined to the males; in others they are present but rudimentary in the female, while they are perfectly developed in both sexes of certain others. In all cases we find that the organs for this purpose differ greatly in closely related forms, and thus show that they are of comparatively recent acquisition.

In the Cicadas the females are mute, and the sound is produced in the male, by the vibration of the lips of the spiracles, which are set into motion by a current of air discharged from the tracheæ. It is increased by a wonderfully complex resonating apparatus, consisting of two cavities covered by scales. This apparatus is present, very much less developed, in the female, but it is never used for producing sound.

The males of the crickets, grasshoppers, and Locustidae, are all remarkable for their musical powers, which are absent in the females. Although these three groups of insects are pretty closely related to each other,

and although the general character of the sound, and its mechanical cause, are essentially alike in all of them, the position and character of the sound-producing mechanism varies greatly.

In the male cricket the under surface of each wing-cover has a row of sharp transverse ridges or teeth, which is rapidly scraped across a projecting ridge on the outer surface of the opposite wing, thus producing the music. First one wing is rubbed over the other, and then the movement is reversed. Both wings are raised a little at the same time, so as to increase the resonance.

In the Locustidæ the opposite wing-covers differ in structure, and their action cannot be reversed, as it is in the crickets. The left wing acts as the bow, and is scraped over the right, which serves as the fiddle. In some forms the posterior part of the pro-thorax is elevated into a sort of resonating dome over the wing-covers. In the grasshoppers the sound is produced in a very different manner. There is usually a long row of nearly a hundred minute teeth on the inner surface of the femur, and this is scraped across the sharp projecting nervures on the wing-covers.

In one South African form the femur is rubbed, not against the wing-cover, but against a notched ridge on the side of the abdomen, and the whole abdomen of the male is distended with air, like a great bladder, to increase the resonance.

The female grasshopper has the stridulating apparatus in a rudimentary condition, and it is interesting to note that the young male is like the adult female in this respect, for Landois states that the teeth on the femora of the female remain throughout life in the condition in which they appear in both sexes during the larval state, but in the male they become fully developed and

acquire their perfect structure at the last moult, when the insect is mature and ready to breed.

Many beetles have rasp-like ridges with fine teeth on certain parts of their bodies, for producing a stridulating noise, by scraping against hard ridges or angles on the adjoining parts. In most stridulating beetles they are equally developed in both sexes: in some they are rudimentary or entirely absent in the female. These organs are situated on widely different parts of the body in different beetles, even when they are very nearly related. In the carrion beetles there are two parallel rasps with fine transverse ribs on the fifth abdominal segment, and they are rubbed against the posterior edge of the wing-cover. In other beetles the rasp is on the dorsal apex of the abdomen. In others it is on the side of the first abdominal segment, and is scraped by ridges on the femur. In others the rasps are on the lower surfaces of the wing-covers, and the edges of the abdominal segments serve as scrapers. In others the horny tip of the abdomen is scraped against a rasp on the wing-covers. In a great number of species of long-horned beetles the rasp is on the meso-thorax, and is rubbed against the pro-thorax. In still other beetles there is a ribbed rasp running obliquely across the coxa of each hind leg, and this is scraped across a specially projecting ridge on one of the abdominal segments. In still others the rasp is on the pro-sternum, and the scraper on the meta-sternum.

In the cases where the stridulating organs are confined to the male, or where they are rudimentary and functionless in the female, we have every reason to believe that the successive variations which have led to their production have originated in males.

In the cases where each sex has inherited them in full perfection, there is, of course, no direct evidence to show

that they have originated in one sex rather than in the other. The organs are essentially alike in structure, whether they are confined to the male or are present in both sexes; and as we have good reason for believing, in the first case, that they have originated in males, and no reason for doubting that they have so originated in the second case, the conclusion that they all have had a male origin certainly has a great probability in its favor.

The great diversity of the males of allied species, as compared with the females, is well shown in those beetles where the males, and not the females, have great horns rising from various parts of the body, as from the head, thorax, clypeus, or the under surface of the body. Darwin gives the following account of these structures: "These horns, in the great family of Lamellicorns, resemble those of various quadrupeds, such as stags, rhinoceroses, etc., and are wonderful both from their size and diversified shapes. The females generally exhibit rudiments of the horns, in the form of small knobs or ridges, but some are destitute of even a rudiment, while in a few others they are almost as well developed in the female as they are in the male. *In almost all cases the horns are remarkable from their excessive variability;* so that a graduated series can be formed, from the most highly developed males to others so degenerate that they can hardly be distinguished from the females. The extraordinary size of the horns, and their widely different structure in closely allied forms, indicate that they have been formed for some important purpose, but their excessive variability in the males of the same species leads to the inference that this purpose cannot be of a definite nature. They do not show evidence of friction as they would if used for ordinary work. They are not usually sharp, and do not seem well adapted for defence,

and they are not known to be used by the males in fighting with each other. The conclusion which best agrees with the fact of the horns having been so immensely yet not fixedly developed, as shown by their extreme variability in the same species, and by their extreme diversity in closely allied species, is that they have been acquired as ornaments."

One fact connected with these horn-like projections gives as clear evidence as could be desired, that the male is more liable to modification in this respect than the female. It sometimes happens that the horns are absent in the males of a species, but present in a number of closely related species, and in such cases we must believe that the departure from the general rule is due to the fact that the species in which they are absent has been recently modified. Now, in such forms the female shows her close relationship to the typical, unmodified, or ancestral form by the possession of rudimentary horns.

Darwin says that it is a highly remarkable fact that, although the males of *Onitis furcifer* do not exhibit even a trace of horns on the upper surface of the body, yet in the females a rudiment of a single horn on the head and of a crest on the thorax are plainly visible. The fact that the female of *Bubas bison*, a form which comes next to *Onitis*, has a similar slight crest on the thorax, while the male has, in the same situation, a great projection, indicates, according to Darwin, that the slight thoracic crest in the female *Onitis* is a rudiment of a projection proper to the male, although it is entirely absent in the male of this particular species. The males of the genus *Onitis* give farther evidence of plasticity, as they have not only lost the horns on the upper surface of the body, but have also acquired new and peculiar ones on the anterior pair of legs, and on

the lower surface of the thorax, and these differ greatly in structure and development in the males of the several species of the genus.

Darwin gives the following illustration to show the remarkable nature of this case: "In most ruminants the males have the horns more developed than the females, and they may be quite small or even absent in the latter sex. Now if a new species of deer or sheep were discovered with the horns entirely absent in the male, but represented by rudiments in the female, we we should have a case like that of *Onitis.* Darwin's illustration would be still more appropriate if we suppose that the male in this newly-discovered deer not only lacks all traces of horns on the head, but has a pair of very peculiar ones on his breast.

In this case we should conclude that the new species is the descendant of a form with horns on the head; that the male sex had become modified, and had lost the horns on the head, and had acquired new ones on the breast, while the female had remained without modification, and had adhered to the ancestral type.

In the Staphylinidae there are horns on the head and thorax, and the males of the same species are extraordinarily variable in this respect. In two genera there are species with polymorphic males, which differ greatly in the development of their horns. In a species of Bledius it is said that, in the same locality, males can be found with the central horn of the thorax very large, but the horns on the head quite rudimentary, while in other males the horns on the head are long, and that on the thorax short.

Darwin devotes more than thirty pages to a discussion of the sexual coloration of butterflies and moths, and the two extracts given below will serve to show that his general

conclusion is in accordance with the demands of our hypothesis, although he himself has given a different explanation, which will be discussed in the next chapter. He says:

"No language suffices to describe the splendor of the males of some tropical butterflies. Even within the same genus we often find species presenting an extraordinary difference between the sexes, while others have their sexes closely alike. Thus in the South American genus Epicalia, Mr. Bates, to whom I am much indebted for most of the following facts, and for looking over this whole discussion, informs me that he knows twelve species, the two sexes of which haunt the same stations, and therefore cannot have been differently affected by external conditions.

"In nine of these species the males rank among the most brilliant of all butterflies, and differ so greatly from the comparatively plain females that they were formerly placed in distinct genera. The females of these nine species resemble each other in their general type of coloration, and likewise resemble both sexes in several allied genera, found in various parts of the world. Hence, in accordance with the descent theory, we may infer that these nine species, and probably all the others of the genus, are descended from an ancestral form which was colored in nearly the same manner. In the tenth species the female still retains the same general coloring, but the male resembles her, so that he is colored in a much less gaudy and contrasted manner than the males of the previous species. In the eleventh and twelfth species, the females depart from the type of coloring which is usual with their sex in this genus, for they are gayly decorated in nearly the same manner as the males, but in a somewhat less degree."

This series of forms seems to show that all twelve species are descended from a form with plain males and plain females; that this character has been retained in both sexes by one species, but that the males have been greatly modified in the other eleven, while in two of them the females have inherited, to an imperfect degree, the modification of the males of their own species, and in the other nine the females have remained stationary and have shown no tendency to inherit the modification of their male parents.

In an allied genus, Eubagis, the males of most of the species are decorated with beautiful metallic tints, in a diversified manner, and differ much from the females. The females throughout the genus, on the other hand, retain a uniform style of coloring, so that they commonly resemble each other much more closely than they resemble their own proper males.

Darwin concludes (*Variation*, Vol. I., p. 378) that "when the sexes of butterflies differ, the male, as a general rule, is the most beautiful, and departs most from the usual type of coloring of the group to which the species belongs. Hence in most groups the females of the several species resemble each other much more closely than do the males," . . . "*and this indicates that the males have undergone a greater amount of modification than the females.*" There are many striking exceptions to this law, which is general but not universal. Certain of the most remarkable exceptions, such as the occurrence of polymorphic female butterflies, and of the various female forms among the social insects, will be discussed at the end of the next chapter.

FISHES.—Darwin gives many instances of difference between the sexes in fishes, and his list might be very greatly increased, but one or two examples will be suf-

ficient to show that these animals follow the rule which prevails in so many other groups of the animal kingdom; that the males are more modified than the females; that the males of allied species differ more than the females, and that the mature male differs more than the mature female from the young.

In many species the male alone is ornamented with bright colors, and he is sometimes provided with curious appendages which do not appear to be of any use whatever for the ordinary purposes of life. When the male *Callionymus lyra* is freshly captured the body is colored with various shades of yellow, with stripes and spots of vivid blue on the head; the dorsal fins are pale brown, with dark longitudinal bands, while the other fins are bluish black; the female fish is of a dingy reddish brown, with the dorsal fin brown and the others white. The sexes differ in many other respects, and the dorsal fin of the male is remarkably and excessively elongated. The sexes are so different from each other that they were for a long time regarded as distinct species, and the male is known as the *gorgeous dragonet,* the female as the *sordid dragonet.*

The males of the various species of this genus differ from each other in these sexual characters, and the young males resemble the adult females in structure and color.

The following extract from Darwin shows how greatly the males of closely allied species differ from each other: "In the male of the *Mollienesia petenensis* the dorsal fin is greatly developed and is marked with a row of large, round, ocellated bright-colored spots, while the same fin in the female is smaller, of a different shape and marked only with irregularly curved brown spots. In the male the basal margin of the anal fin is also a little produced and dark colored. In the male of an allied form, the

Xiphophorus Hellerini, the inferior margin of the anal fin is developed into a long filament which is striped with bright colors. This filament does not contain any muscles, and apparently cannot be of any direct use to the fish. As in the case of *Callionymus* the males while young resemble in color and structure the adult females."

Darwin discusses the question whether, when the male differs in a marked manner from the female in color or in other ornaments, he alone has been modified with the variations inherited only by his male offspring, or whether the female has been specially modified and rendered inconspicuous for the sake of protection, and he concludes that *with most fishes in which the sexes differ in color or in other ornamental characters, the males originally varied.*

LIZARDS. — Among lizards the sexes often differ greatly in various external characters, and the male sex is in almost every case the one which is peculiar. Among the many examples given by Darwin I quote the following:

"In *Anolis cristatellus* the male is furnished with a crest which runs along the back and tail and can be erected at pleasure, but of this crest the female does not exhibit a trace, although in other species the female does have an imperfect crest, which is much less developed than it is in the male. In the genus *Sitana* the males alone are furnished with a large throat pouch, which can be folded up like a fan, and is colored blue, black and red during the pairing season. The female does not possess even a rudiment of this appendage. The male of *Ceratophora aspera* has a long appendage half as long as his head on the tip of his snout. In a second species of the same genus a terminal scale forms a minute horn on

the summit of this appendage, and in a third species the whole appendage is converted into a horn. In the females of all these species and in the young males the appendage is very minute. The male *Chameleon bifurcus* has two great solid bony projections, covered with scales, in the upper part of the skull. The male *Chameleon Owenii* has three great bony horns on his head. These bony horns are covered with a smooth sheath of integument, so that they are strikingly like those of a bull or a goat. In the females and young of both species these appendages are rudimentary."

BIRDS.—The sexual characteristics of birds are most diversified and conspicuous, and most persons, even those who are not naturalists, know enough of this subject to agree that the males are as a rule much more modified than the females, and it will not be necessary to devote very much space to this group. Darwin has devoted more than two hundred pages to the discussion of the differences between male and female birds, and he has brought together an array of facts all tending to show that male modification is the rule, while female modification is comparatively rare, and although it is true that he gives another explanation of the phenomena, an explanation which will be discussed in the next chapter, yet every reader of his essay must be convinced of the correctness of his conclusion, p. 227, "that weapons for battle, organs for producing sound, ornaments of many kinds, bright and conspicuous colors, *have generally been acquired by the males*, . . . the females and the young being left comparatively but little modified."

This conclusion will be accepted without question by all who are familiar with the subject, and it is hardly necessary to dwell upon it, but the great diversity of the sexual differences in birds demands that in a general

review of the subject they should receive some little notice.

Darwin says: "Male birds sometimes, though rarely, possess special weapons for fighting with each other. They charm the females by vocal and instrumental music of the most various kinds. They are ornamented by all sorts of combs, wattles, protuberances, horns, air-distended sacs, top-knots, naked shafts, plumes and lengthened feathers, gracefully springing from all parts of the body. The beak and naked skin about the head and the feathers are often gorgeously colored. The males sometimes pay their court by dancing, or by fantastic antics, performed either on the ground or in the air. In one instance, at least, the male emits a musky odor, which we may suppose serves to charm or excite the female. The ornaments are wonderfully diversified. The plumes on the front or back of the head consist of variously shaped feathers, sometimes capable of erection or expansion, by which their beautiful colors are fully displayed. Elegant ear-tufts are occasionally present. The head is sometimes covered with velvety down like that of the pheasant, or is naked and vividly colored, or supports fleshy appendages, filaments and solid protuberances. The throat also is sometimes ornamented with a beard, or with wattles or caruncles. Such appendages are generally brightly colored, and no doubt serve as ornaments, though not always ornamental in our eyes: for while the male is in the act of courting the female, they often swell and assume more vivid tints, as in the case of the male turkey. At such times the fleshy appendages about the head of the male Tragopan pheasant swell into a large lappet on the throat and into two horns, one on each side of the splendid top-knot, and these are then colored of the most intense blue which I have ever beheld.

The African hornbill inflates the scarlet bladder-like wattle on its neck, and with its wing drooping and tail expanded makes quite a grand appearance. Even the iris of the eye is sometimes more brightly colored in the male than in the female, and this is frequently the case with the beak, for instance in our common blackbirds. In *Buceros corrugatus*, the whole beak and immense casque are colored more conspicuously in the male than in the female, and the oblique grooves upon the sides of the lower mandible are peculiar to the male sex. The males are often ornamented with elongated feathers or plumes, springing from almost every part of the body. The feathers on the throat and breast are sometimes developed into beautiful ruffs and collars. The tail feathers are frequently increased in length, as we see in the tail of the Argus pheasant. The body of this latter bird is not larger than that of a fowl, yet the length from the end of the beak to the extremity of the tail is no less than five feet three inches. . . . Nor need much be said on the wonderful differences of color between the sexes, or on the extreme beauty of the males of many birds. The common peacock offers a striking instance. Female birds of Paradise are obscurely colored and destitute of all ornaments, while the males are probably the most highly decorated of all birds, and in so many ways that they must be seen to be appreciated. The elongated and golden orange plumes which spring from beneath the wings of the *Paradisea apoda*, when vertically erected and made to vibrate, are described as forming a sort of halo, in the centre of which the head looks like a little emerald sun, with its rays formed by the two plumes. In another most beautiful species the head is bald and of a rich cobalt blue crossed by several lines of black velvety feathers. Male humming birds almost vie with birds

of Paradise in their beauty, as every one will admit who has seen Mr. Gould's splendid volumes in his rich collection. It is very remarkable in how many different ways these birds are ornamented. Almost every part of the plumage has been taken advantage of and modified. . . . . When the sexes of birds differ in beauty, in the power of singing, or in producing instrumental music, it is almost invariably the male which excels the female."

This extract is enough to show the wonderful diversity of the characteristics of male birds, and the following examples bring out very prominently the fact that male birds of allied species often differ greatly in their sexual characters, while the females are very much alike. In the South American bell-birds the females of the four species resemble each other very closely, and are of a dusky green color, while the male of one species is pure white; in a second species white with the exception of a large space of naked skin on the throat and round the eyes, which during the breeding season is of a fine green color, while in a third species only the head and neck of the male are white and the rest of the body chestnut-brown. In one species the male alone is provided with three filamentous projections half as long as the body, one rising from the base of the beak and the others from the corners of the mouth, while in another species the male has a spiral tube nearly three inches in length which rises from the base of the beak and is jet black dotted over with minute downy feathers. In the Indian chats, honeysuckers, shrikes, kingfishers, Kallij pheasants, and tree partridges, the males of allied species from distinct countries are quite different from each other, while the females and the young of both sexes are indistinguishable.

In the cases where the females of allied species do differ the difference is rarely so great as between the males. Darwin says: "We see this clearly in the whole family of the Gallinaceæ: the females for instance of the common and Japan pheasant, and especially of the gold and Amherst pheasant, of the silver pheasant and the wild fowl, resemble each other very closely in color, while the males differ to an extraordinary degree. So it is with the *Cotingidae Fringillidae* and many other families. *There can indeed be no doubt that as a general rule the females have been modified to a less extent than the males.*" (*Variation*, Vol. II. p. 184.)

As regards the relation between the young and the adult, the general rule is that when the sexes differ the young of both sexes in their first plumage resemble the adult female as they do in the common fowl or the peacock, or else they resemble her more closely than they do the adult male.

Darwin says that innumerable instances of this law could be given in all orders, but that it will suffice to call to mind the common pheasant, duck, and house sparrow.

There are a few cases in which the young male is like the adult male, and the young female like the adult female, and there are also a few cases where the young of both sexes resemble the adult male, but the difference between the sexes is never, in this case, very great, and in stances are so rare that Darwin, who says that he has recorded all he could find, gives only nine. In his summary he says: "We thus see that the cases in which female birds are more conspicuously colored than the males, with the young in their immature plumage resembling the adult males instead of the adult females, *are not numerous,* though they are distributed in various orders. The

amount of difference between the sexes is also *incomparably less* than that which frequently occurs in the last class; *so that the cause of the difference, whatever it may have been, has acted upon the females in the present class either less energetically or less persistently than on the males in the last class.* (*Descent of Man*, II. p. 198.)

MAMMALS.—Among the mammalia the sexes often differ in their weapons of offence and defence, as we see in the deer, when the horns are usually absent in the female; in their voices, as in the case with the cow and bull; in odor, as goats for example, and in the musk deer, where both the musk-producing organ and other organs of a similar character are confined to the male; in color, as in many antelopes, and in the character and distribution of the hair, as we may see by comparing the lion with the lioness, or the human male with the human female.

A little thought will show that among the mammals, as in other groups of the animal kingdom, the males are more modified than the females.

Thus man differs from woman by the possession of a beard, but the boy resembles the girl or the mature female, thus showing that the human race is influenced by the general law of which we have seen the evidence in so many groups of animals, and that the adult female is more like the young of both sexes than the adult male. So, too, the young stag, or the young male goat, resembles the adult female in the absence of horns.

The fact that different human races are characterized by the presence or absence of a beard in the males, and that the horns of different species of deer differ very greatly, shows that the males of allied species of mammals differ more than the females.

Among the mammalia we sometimes find that the

male has been modified by the acquisition of new structures, while in other cases organs common to both sexes and to great groups have become changed in the male, but have remained comparatively unmodified in the female.

The spurs on the leg of the male Ornithorinchus may, perhaps, be regarded as a case of the first kind, as may also the horns of the rhinoceros, which are longer and more important in the male than they are in the female, while the great tusks of the boar are organs which must have been present in both sexes of the remote ancestors, although they have recently undergone great change in the male.

No one who will compare the head of the common boar with that of the male Babyrusa, the male wart-hog, and the male river-hog, can doubt that the males of these allied species differ much more than the females.

In some cases certain teeth of the male are so greatly modified that they must be regarded as new organs. This is true of the narwhal, in which one of the teeth is greatly elongated, and forms a long, spirally-twisted spear, nine or ten feet long, while the corresponding tooth in the male, and both teeth in the female, are rudimentary.

The tusks of the male walrus, and those of the male elephant, are greatly modified teeth, but they differ so greatly from ordinary teeth that they are almost as truly new organs as the horns of ruminants.

It is interesting to note how greatly the various races of elephants differ in the development of the tusks. In Ceylon they are never found in the females, and they occur in only about one per cent. of the males. In India they occur in all or nearly all the males, but in the males alone, while in Africa the female usually has small tusks.

The same thing is true of the horns of ruminants. In the hollow-horned species, as in cattle, they are not at all uncommon in the females, although they are usually much less important than they are in the males. Among the antelopes the females of some species have horns like the males; in other species they are somewhat smaller in the female than they are in the male; in others they are large in the male, but rudimentary in the female, while in others they are entirely absent in the female.

In female deer they are usually absent entirely, but in some they are rudimentary, and in the female reindeer they are fully developed. It is interesting to note that in females which normally lack them, they may be developed as the result of injury or disease of the reproductive organs, and that their development in the male may be arrested by castration.

CHAPTER IX.

THE EVIDENCE FROM SECONDARY SEXUAL CHARACTERS CONTINUED. — THE CAUSE OF THE EXCESSIVE MODIFICATION OF MALE CHARACTERS.

The Explanation of Daines Barrington and Wallace—Reasons for considering it inadequate—Darwin's explanation—History of domesticated races shows that this does not go to the root of the matter—The view that the male is more exposed than the female to the action of selection—A more fundamental explanation is needed—This is furnished by our theory of heredity—Special difficulties—Summary.

THE sexual characteristics of animals have been made the subject of considerable discussion by various naturalists, and among birds especially there have been many attempts to explain why the female has not acquired the same ornaments as the male.

The Explanations of Daines, Barrington and Wallace.

Wallace points out that conspicuous ornaments and brilliant plumage would render the female bird prominent while incubating, and would thus enable enemies to detect the presence of the nest. He believes that sinceincubating females are exposed to this danger, natural selection has acted, by the destruction of the most conspicuous females, to gradually produce races in which the females have nothing to render them conspicuous.

In 1773 the Hon. Daines Barrington called attention (*Phil. Trans.* 1773, p. 164) to the fact that singing birds are all small, and he believes that this arises from

the difficulty larger birds would have in concealing themselves if they called the attention of their enemies by loud notes. He also says that he conceives it is for the same reason that no hen bird sings, because this talent would be still more dangerous during incubation, and he suggests that the inferiority of the female bird in point of plumage may be due to the same cause.

This argument, that the dull color and lack of ornament in female birds is a direct adaptation to their peculiar life, has been elaborated by Wallace. (*On Natural Selection*, p. 231.) He says that in the struggle for existence incessantly going on, protection or concealment is one of the most general and most effectual means of maintaining life, and it is by modifications of color that this protection can be most readily obtained, since no other character is subject to such numerous and rapid variations. He says that, as a general rule, the female butterfly is of dull and inconspicuous colors, even when the male is most gorgeously arrayed, and that in all these cases the difference can be traced to the greater need of protection for the female, on whose continued existence, while depositing her eggs, the safety of the race depends.

Since a male insect is, by its structure and habits, less exposed to danger, it does not need any special means of protection, as the female does, to balance the greater danger to which she is exposed, and Wallace believes that on account of this danger, and because of her greater importance to the existence of the species, the female insect always acquires this protection in one way or another through the action of natural selection.

He also says that "the female bird, while sitting on her eggs in an uncovered nest, is much exposed to the attacks of enemies, and any modification of color which

rendered her more conspicuous would often lead to her destruction, and that of her offspring. All variations in this direction in the female would therefore, sooner or later, be eliminated, while such modifications as rendered her inconspicuous by assimilating her to surrounding objects, as the earth or the foliage, would, on the whole, survive the longest, and thus lead to the attainment of those brown or green and inconspicuous tints which form the coloring (of the upper surface at least) of the vast majority of female birds which sit upon open nests." As a proof that this is the true explanation of the dull plumage and lack of ornaments in so many female birds, he states that wherever the nest is domed or covered, or so placed as to conceal the sitting bird, the plumage is strikingly gay and conspicuously colored in both sexes; but that in those species where there is a strong contrast in colors, and the male is gay and conspicuous, while the female is dull and obscure, the nest is open, and the sitting bird is exposed to view.

Reasons for Holding that this Explanation is Inadequate.

The argument of Wallace, which is fully stated in the essay above quoted, is briefly, that the dull plumage of so many female birds, as contrasted with the gay colors of the males, has been directly acquired in the females by the destruction of the most conspicuous ones, and the natural selection of the inconspicuous varieties.

Darwin has discussed it at length in his essay on sexual selection, and has given many reasons for refusing to give it unqualified acceptance, but I will give here a few additional reasons for believing that the phenomena in question depend upon some more fundamental law. In the first place, we must bear in mind that,

even among birds, the male differs from the female by the possession of numerous secondary sexual characters besides brilliant plumage, and that many of these, like the spurs of male Gallinaceæ, are not at all conspicuous. Bechstein (*Naturgesch Deutschland*) says that a breed of fowls formerly existed in Germany in which the hens were furnished with spurs, but that they could not be allowed to sit on their own eggs, as, although they were good layers, the spurs disturbed the nest and broke the eggs; and it might perhaps be urged that the absence of spurs in the females of wild species of Gallus may be due to the selection, for this reason, of females without spurs, but we must recollect that natural selection acts upon every part of the organism, and would, if the female were as liable as the male to give rise to hereditary variations, have acted, during the evolution of spurs, to bring the structure and habits of the female into harmony with these new weapons, so that she could enjoy their protection without injury to her eggs.

Darwin says that when we think of the multitude of birds which with impunity gladden the country with their songs during the spring, it does not seem probable that the females have been saved from acquiring this power on account of the danger to which they would have been exposed by attracting the attention of birds and beasts of prey.

If female birds have had the power of song, it would certainly seem simpler for them to have acquired the habit of restraining their voices in dangerous places than to suppose that the power has been removed by natural selection.

Wallace's view fails to account for the fact that the plumage of allied species of females is, as a rule, much more alike than that of the males; and this fact is quite

inexplicable if the dull colors of the females are due to direct modification by natural selection.

Again, we must recollect that among the lizards, where the females do not incubate, the males are often much more conspicuously colored than the females, and the females of allied species are more alike than the males. Here the dull colors of the females as compared with those of the males cannot be accounted for by the natural selection of those females which are least exposed to danger during incubation.

Among fishes the same rule is adhered to, and the males are usually more conspicuous than the females, and here the female is certainly no more exposed to danger than the male. "As far as there is any difference, the males, from being generally of smaller size, and from wandering about more, are exposed to greater danger than the females; and yet when the sexes differ, the males are almost always the most conspicuously colored. The ova are fertilized immediately after being deposited, and when this process lasts for several days, as in the case of the salmon, the female during the whole time is attended by the male. After the ova are fertilized they are, in most cases, left unprotected by both parents, so that the males and females, as far as oviposition is concerned, are equally exposed to danger, and both are equally important for the production of fertile ova; consequently the more or less brightly colored individuals of either sex would be equally liable to be destroyed or preserved, and both would have an equal influence on the colors of their offspring or the race." (Darwin, *Sexual Selection,* Vol. II, p. 19.)

The male stickleback does all the work of building the nest, and after the eggs are laid and fertilized he drives the females away, and performs for a long time

the duties of a nurse with exemplary care and vigilance, gently leading back the young to the nest when they stray too far. Yet the male is more brilliantly colored than the female, and his colors are especially brilliant and conspicuous during the breeding season.

I shall show farther on that the males of domesticated breeds of fowls and pigeons are more conspicuous and diversified than the females, but as fancy pigeons are reared in confinement, and are protected from every danger, this cannot be due to the natural selection of the best-protected females.

We must conclude, then, that the brilliant plumage of male birds is due to some more general and fundamental cause than the one proposed by Wallace, since female reptiles which do not incubate, and female fishes which are even less exposed to danger than the males, and female domesticated birds which are thoroughly protected from enemies, all follow the same law.

The fact that many structures which are not at all conspicuous are confined, like gay plumage, to male birds, also indicates the existence of an explanation more fundamental than the one proposed by Wallace, and this latter explanation gives no reason why the females of allied species should so often be almost exactly alike when the males are very different.

Darwin's Explanation.

Darwin has given a different explanation, and he believes that the greater modification of males through. out the animal kingdom is chiefly due to sexual selection. He has devoted more than five hundred pages to the development of this idea in his essay on sexual selection (*Descent of Man,* Part II.), and he has marshalled an overwhelming array of facts with mas-

terly skill. The attempt to point out within the limits of a single chapter the errors of his conclusion is beset with many difficulties, and I shall be compelled to treat the subject with brevity, and to leave unsaid much which might be urged did space permit.

As an introduction to the discussion of the subject, I shall quote Darwin's statement of the meaning of the term "sexual selection." He says: "This depends on the advantage which certain individuals have over other individuals of the same sex and species in exclusive relation to reproduction. When the two sexes differ in structure in relation to different habits of life, they have, no doubt, been modified through natural selection, accompanied by inheritance limited to one and the same sex. So, again, the primary sexual organs, and those for nourishing and protecting the young, come under the same head; for those individuals which generated or nourished their offspring best, would leave, *cæteris paribus*, the greatest number to inherit their superiority; while those which generated or nourished their offspring badly, would leave but few to inherit their weaker powers. As the male has to search for the female, he requires for this purpose organs of sense and locomotion, but if these organs are necessary for the other purposes of life, as is generally the case, they will have been developed through natural selection. When the male has found the female he sometimes absolutely requires prehensile organs to hold her; thus Dr. Wallace informs me that the males of certain moths cannot unite with the females if their tarsi or feet are broken. . . . When the two sexes follow exactly the same habits of life, and the male has more highly developed sense organs or locomotive organs than the female, it may be that these in their perfect state are indispen-

sable to the male for finding the female; but in the vast majority of cases they serve only to give one male an advantage over another, for the less well-endowed males, if time were allowed them, would succeed in pairing with the females; and they would in all other respects, judging from the structure of the female, be equally well adapted for their ordinary habits of life. In such cases sexual selection must have come into action, for the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone. It was the importance of this distinction which led me to designate this form of selection as sexual selection. So, again, if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been forfeited through sexual selection, that is, by the advantage acquired by certain males over their rivals. But in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection. . . . There are many structures and instincts which must have been developed through sexual selection, such as the weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals—their courage and pugnacity—their ornaments of many kinds—their organs for producing vocal or instrumental music, and their glands for emitting odors; most of these latter structures serving only to allure or excite the females. That these characters are the result of sexual and not of ordinary selection is clear, as unarmed, unornamented, or unattractive males would succeed equally well in the battle for life, and in leav-

ing a numerous progeny, if better endowed males were not present. We may infer that this would be the case, for the females, which are unarmed and unornamented, are able to survive and procreate their kind. Secondary sexual characters of the kind just referred to will be fully discussed in the following chapters, as they are, in many respects, interesting, but more especially as they depend on the will, choice, and rivalry of the individuals of either sex.

"When we behold two males fighting for the possession of the female, or several male birds displaying their gorgeous plumage and performing the strangest antics before an assembled body of females, we cannot doubt that, though led by instinct, they know what they are about, and consciously exert their mental and bodily powers. In the same manner as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature, and have led to the improvement of the natural breed or species. Through repeated deadly contests, a slight degree of variability, if it led to some advantage, however slight, would suffice for the work of sexual selection; and it is certain that secondary sexual characters are eminently variable.

"In the same manner as man can give beauty, according to his standard of taste, to his male poultry—can give to the Sebright bantam a new and elegant plumage, an erect and peculiar carriage—so it appears that in a state of nature female birds, by having long selected the more attractive males, have added to their beauty. . . . It is certain that with almost all animals there is a struggle between the males for the possession of the fe-

males. . . . Of the males the strongest, and, with some species, the best armed, drive away the weaker males; and the former would then unite with the more vigorous and best nourished females, as these are the first to breed. Such vigorous pairs would surely rear a larger number of offspring than the retarded females, which would be compelled to unite with the conquered and less powerful males; and this is all that is wanted to add, in the course of successive generations, to the size, strength, and courage of the males, or to improve their weapons. But in a multitude of cases the males which conquer other males do not obtain possession of the females independently of choice on the part of the latter. The courtship of animals is by no means so simple and short an affair as might be thought. The females are most excited by, or prefer pairing with, the more ornamented males, or those which are the best songsters, or play the best antics; but it is obviously probable, as has been actually observed in some cases, that they would at the same time prefer the most vigorous and lively males. . . . And this apparently has sufficed during a long course of generations to add not only to the strength and fighting power of the males, but likewise to their various ornaments or other attractions. . . . To sum up on the means through which, so far as we can judge, sexual selection has led to the development of secondary sexual characters: It has been shown that the largest number of vigorous offspring will be reared from the pairing of the strongest and best armed males, which have conquered other males, with the most vigorous and best-nourished females, which are the first to breed in the spring. Such females, if they select the most attractive and, at the same time, vigorous males, will rear a larger number of offspring than the retarded females,

which must pair with the less vigorous and less attractive males. So it will be if the more vigorous males select the more attractive and, at the same time, healthy and vigorous females; and this will especially hold good if the male defends the female and aids in providing food for the young. The advantage thus gained by the more vigorous pairs in rearing a larger number of offspring has apparently sufficed to render sexual selection efficient."

The Study of Domesticated Races shows that this Explanation does not go to the Root of the Matter.

This long extract will, I hope, fully explain to those readers who are not familiar with Darwin's essay, the nature of sexual selection. It will be seen that he attributes the greater modification of the males as compared with the females, in most of the groups of animals where the sexes differ, to the fact that the males have struggled with each other for the possession of the females, or have been chosen by the females. This process, long continued, is believed to have resulted in the perpetuation of the strongest, best armed, or most attractive males.

I fully acknowledge the great potency of sexual selection, and believe with Darwin that it must act in essentially the manner described by him, but I do not believe that it goes to the root of the matter.

Fortunately there is a simple experimental test which is easily tried and gives a satisfactory solution of the question whether the phenomena do or do not depend upon something more fundamental than the exposure of the male to the action of selection.

If we take animals in which the sexes differ but little, and prevent them from following their own inclinations,

and pair them without any reference to their own preferences, and continue this for a number of generations, until we have produced a number of divergent races or breeds; if we then find that the males of these breeds differ more from each other than the females, we must conclude that there is, behind the action of selection, some more deep-seated law, which determines that males shall, as a rule, be more modified than females.

Domesticated Pigeons.

The study of domesticated pigeons is extremely interesting in this connection, for it shows conclusively that the tendency which we have shown to exist in nearly all groups of bisexual animals, the tendency of the male to deviate more than the female from the typical structure of allied forms, cannot be attributed exclusively to the fact that the male is more exposed than the female to the action of either sexual or ordinary selection.

There are more than two hundred wild species of the pigeon family, and throughout the whole group there is an almost total absence of external difference between the sexes. In a few species the plumage is somewhat more brilliantly colored in the male than it is in the female, and it is stated that in one species, *Carpophaga oceanica,* the excrescence at the base of the beak is a sexual character, but these differences between the sexes are slight and exceptional.

In domesticated pigeons, on the contrary, the sexes often differ considerably, and it is a remarkable fact that here, as in so many other groups of the animal kingdom, "the characteristics of the different breeds are often most strongly displayed in the male bird." (Darwin, *Variation,* Vol. I. p. 199.) In many cases the sexes are

alike; thus the female trumpeter has a tuft like that of the male, and the hood of the Jacobin and the frill of the turbit are alike in both sexes; but wherever the sexes do differ the males are, as a rule, more modified than the females.

In all ordinary domesticated breeds as well as in most wild species, the number of tail-feathers is twelve, but in the fan-tail breed there are from thirty to forty, and they are permanently expanded like a fan. We must believe that this deviation from the typical number of tail-feathers in the pigeon family is due to recent modification, and we find that the number is often much greater in the male fan-tail than it is in the female.

The pouter pigeon is a very remarkable domestic breed. All domestic pigeons have some slight power of inflating the crop, but this power is so greatly developed in the pouter breed that the bird is able to blow himself up like a balloon, and Darwin says that after one of his pouters had swallowed a good meal of peas, he could hear the peas rattle as if in a bladder as the bird flew through the air with its crop inflated. Darwin says that the males pout more than the females, and glory in this power, and strut about puffed up with wind and pride. He also says that it is a very unusual thing for the female to excel in pouting. We must therefore believe that the male pouter has departed further than the female from ordinary pigeons.

The tumbling habit of tumbler pigeons is perhaps the most remarkable of all the hereditary modifications of domestic animals which man has produced. The following account of the English tumbler is quoted by Darwin from Brent: "Every few seconds over they go, one, two, or three somersaults at a time. Here and there a bird gives a very quick and rapid spin, re-

volving like a wheel, though they sometimes lose their balance and make a rather ungraceful fall, in which they occasionally hurt themselves by striking some object. They begin to tumble almost as soon as they can fly; at three months old they tumble well but still fly strong; at five or six months they tumble excessively, and in the second year they mostly give up flying on account of their tumbling so much and so close to the ground. Some fly round with the flock, throwing a clean somersault every few yards, till they are obliged to settle from giddiness and exhaustion. These are called air-tumblers, and they commonly throw from twenty to thirty somersaults in a minute, each clear and clean. I have one red cock that I have on two or three occasions timed by my watch, and counted forty somersaults in the minute. Others tumble differently. At first they throw a single somersault, then it is doubled till it becomes a continuous roll, which puts an end to flying, for if they fly a few yards, over they go, and roll till they reach the ground. Thus I had one kill herself, and another broke his leg. Many of them turn over only a few inches from the ground, and will tumble two or three times in flying across their loft. These are called house-tumblers, from tumbling in the house."

The tumbling habit is shared by both sexes, but as in the case of the pouter, it is the male which excels.

The carrier and barb races of domestic pigeons are characterized by the presence of naked carunculated skin over the beak and around the eyes, and in both of these races this feature is most pronounced in the males. These illustrations are sufficient to show that the distinctive characteristics of each breed of domesticated pigeons are either alike in both sexes, or else most de-

veloped in the males, and that the males of allied breeds differ from each other more than the females.

The individuals of choice breeds of domestic pigeons are not allowed to follow their own inclinations and to pair at will, but they are very carefully watched by the breeder, for reasons which have no reference to the inclinations of the birds, so that there is no chance for sexual selection, nor does the breeder confine his attention to the male sex especially, but seeks to improve the female as well as the male; and Mr. Eaton asserts in his "Treatise on the Almond Tumbler" that a hen tumbler would be worth twice as much money as a cock if she had the characteristics of the breed equally well developed.

We find, then, that among the two hundred or more wild species of the pigeon family, where sexual selection has every chance to act, there is no great difference between the sexes; but that in the more valuable domesticated breeds, where all choice is precluded, and sexual selection out of the question, the males are, as a rule, more modified than the females whenever the sexes differ. We must therefore conclude that the greater modification of the males, in pigeons at least, is not due to the fact that the male is more exposed than the female to the action of selection, but that the male has more tendency than the female to depart from the ancestral type. In pigeons, at least, we must believe that something within the animal determines that the male should lead and the female follow, in the evolution of new breeds.

Domesticated Animals in General.

When we study other domesticated animals in the same way, we find that in some cases, as in horses, there is little difference between the sexes, and in other cases

the efforts of the breeder are directed towards a peculiarity of one or the other sex, as when cattle are reared for the sake of their milk, or when fowls are kept for fighting, or for their eggs; but whenever the sexes do differ we find that the same law exists, and that the males of allied races differ from each other more than the females. Regarding sheep, Darwin says that there is a strong tendency for characters which have been acquired under domestication to become attached exclusively to the male sex, or to be much more highly developed in the male than in the female. As illustrative of this law he refers, among other instances, to the fact that the accumulation of fat in the fat-tailed sheep of the plains of India is greater in the male than in the female, and the mane of the African maned race is far more developed in the ram than in the ewe.

Among fowls, every one is familiar with the fact that the males of different breeds are, as a rule, much more different than the females, and that most of the breeds are distinguished from each other by peculiarities in organs which, like the comb, spurs, and long tail-feathers, are confined to the male. As a rule there is considerable difference between the sexes of fowls, but exceptions are not at all unusual, and in many breeds the sexes can hardly be distinguished. The males and females of the gold and silver laced Sebright bantam can be barely distinguished from each other, except by the comb, wattles, and spurs, for they are colored alike, and the males have not hackles, nor the flowing, sickle-like tail-feathers. In one breed of game fowls the males and females are said to resemble each other so closely that the cocks have often mistaken their hen-feathered opponents in the cock-pit for real hens, and have lost their lives by the mistake, for although the cock is dressed in

the feathers of the hen, he retains all his courage and high spirit.

In a few cases the females of allied breeds differ more than the males, and Darwin refers to two strains of black-breasted red games, in which the cocks were so much alike that they could not be distinguished, while the hens were partridge-brown in the one case and fawn-brown in the other. The pencilling which is characteristic of the Hamburg hen is almost absent in the male, but as a rule the various breeds of fowls are distinguished by peculiarities of organs which are almost or entirely confined to the males.

Of the comb Darwin says that it differs much in the various breeds, and its form is eminently characteristic of each kind with the exception of the Dorkings. A single deeply serrated comb is the typical and most common form. It differs much in size, being immensely developed in Spanish fowls; and in a local breed called Redcaps, it is sometimes upwards of three inches in breadth at the front, and more than four inches in length, measured to the end of the peak behind. In some breeds the comb is double, and when the two ends are cemented together it forms a "cap comb;" in the "rose comb" it is depressed, covered with small projections, and produced backwards; in the horned and Créve-Cœur fowl it is produced into two horns; it is triple in the pea-combed Brahmas, short and truncated in the Malays, and absent in the Guelderlands. In the tasselled game a few long feathers arise from the back of the comb, and in many breeds a crest of feathers replaces the comb. The crest, when little developed, arises from a fleshy mass, but when much developed, form a hemispherical protuberance of the skull. In the best Polish fowls it is so largely developed that the birds can hardly pick up their

food, and they are said to be particularly liable to be struck by hawks.

With reference to variation in the plumage of the male fowl Darwin says (*Variation*, p. 307): "As in some orders of birds the males display extraordinarily shaped feathers, such as naked shafts with disks at the end, etc., the following case may be worth giving. In the wild *Gallus bankiva*, and in our domestic fowls, the barbs which arise from each side of the extremities of the hackels are naked or not clothed with barbules, so that they resemble bristles; but Mr. Brent sent me some scapular hackels from a young Birchen Duckwing game-cock, in which the naked barbs became densely reclothed with barbules towards their tips, so that these tips, which were dark colored with a metallic lustre, were separated from the lower parts by a symmetrically-shaped transparent zone formed of the naked portions of the barbs. Hence the colored tips appeared like little separate metallic disks. The sickle feathers in the tail, of which there are three pair, and which are eminently characteristic of the male sex, differ much in the various breeds. They are scymater-shaped in some Hamburgs, instead of being long and flowing as in the typical breeds. They are extremely short in the Cochins, and are not at all developed in Hennies. They are carried, together with the whole tail, erect in Dorkings and games, but droop much in Malays and some Cochins. Sultans are characterized by an additional number of lateral sickle feathers. The spurs vary much, being placed higher or lower on the shank; being extremely long and sharp in games, and blunt and short in Cochins."

The number of the spurs varies, some fowls having as many as five on each leg; their position on the leg also varies in different breeds.

These extracts are sufficient to show that organs which are confined to the cock are especially variable, and that the characteristics of each breed are chiefly modifications of their male parts.

It is therefore evident that the males of the various breeds are as a rule much more different from each other than the females, in fowls, as well as in sheep, pigeons and other domestic animals. The rule is by no means universal, however, and there are a few remarkable exceptions. I have already mentioned two cases of black-breasted red game fowls, in which the females were quite distinct, while the males of the two forms could not be distinguished. The breed of domestic ducks known as the Call Duck is remarkable for its small size and from the extraordinary loquacity of the female, while the drake only hisses like ordinary drakes.

Darwin gives (*Variation,* Vol. I. p. 309) an interesting account of the origin of the crest in Polish fowls. He says that in most fowls head ornaments of all kinds are more fully developed in the male than in the female; but in Polish fowls the crest or top-knot, which in the male replaces the comb, is equally developed in both sexes. "In certain sub-breeds, which from the hen having a small crest are called lark-crested, a single upright comb sometimes almost entirely takes the place of the crest in the male. From this latter case, and from some facts presently to be given with respect to the protuberance of the skull in Polish fowls, the crest in this breed ought perhaps to be viewed as a feminine character which has been transferred to the male. . . . At the present day all the breeds of Polish fowls have the great bony protuberance on their skulls, which includes part of the brain and supports the crest, equally developed in both sexes. But formerly in Germany the skull of

the hen alone was protuberant. Blumenbach, who particularly attended to abnormal peculiarities in domestic animals, states, in 1813, that this was the case; and Bechstein had previously, in 1793, observed the same fact. This latter author . . . . expressly states that he never observed this protuberance in male fowls. Hence there can be no doubt that this remarkable character in the skulls of Polish fowls was formerly in Germany confined to the female sex, but has now been transferred to the males, and has thus become common to both sexes."

These few cases are clearly exceptional, and the study of domesticated animals shows us that, as a rule, the males of allied breeds, like the males of wild species, are more different from each other than the females. We cannot attribute this difference to sexual selection, for most of our domesticated animals, especially those of pure blood, are prevented by man from following their own inclination in the selection of mates. Neither can we assert that man has devoted especial attention to the selection and modification of males, and has aimed at changes in those organs which are most developed in males, for, among pigeons at least, the opposite of this is the case, and a female bird of equal excellence is more valued than a male. We are thus forced to conclude not only that "among domesticated animals the male is more variable than the female" (Darwin, *Sexual Selection*, Vol. I. p. 266), but also that organs which are confined to males, or unusually developed in them, are more apt than organs which are confined to females, to transmit their variations, and thus to give rise to hereditary race modifications. As our domesticated races show, by their close similarity to natural species, that the causes which have produced them are very similar to those which have acted upon wild organisms, we are justified

in doubting, from the analogy of domesticated animals, whether the excessive modification of the males of wild animals is due entirely to the fact that males are more exposed than females to the action of selection. As the study of domesticated races leads us to the conclusion that something within the animal compels the male to lead and the female to follow in the evolution of new breeds, we must believe that a similar law regulates in the same way the evolution of wild organisms. The study of domesticated races, like the study of wild species, also compels us to believe that this law is not immutable, but that variations which originate in a female may become hereditary, although this is somewhat rare, as compared with the hereditary establishment of male modifications.

The View that the Male is more Exposed than the Female to the Action of Selection.

According to Darwin the excessive exposure of the male to the action of selection, natural and sexual, is the cause of his great modification. He points out that the distinctive characters of the male are, in many cases at least, of especial use to him, as a male, and he shows that the individuals which possess these peculiarities are benefited by them, and have therefore been preserved, while the females, deriving no advantage from them, have not been thus selected.

No one can doubt the truth of this statement, but it does not go to the root of the matter. The question is not how peculiarities useful to the male alone have been restricted to that sex, but why the female has not acquired another set of characteristics to fit her for her peculiar needs. No one can doubt that a hen might have special organs, as useful to her for the care and pro-

tection of her brood, and for her own defence while incubating, as the cock's spurs and ornaments are in another way to him: nor can we doubt that such organs would be preserved and perfected by natural selection if proper variations should appear and should become hereditary.

Among the mammalia the peculiar organs of the male, his so-called secondary sexual characters, are often of great use to him in ways which are not connected with reproduction. This is especially true of his weapons of offence, for the bull not only uses his horns in fighting with other males for the females, but also in protecting himself and the rest of the herd from enemies. The elephant uses his tusks in many ways. He tears down trees with them for the sake of the foliage, and he rips open palm trees in order to obtain the nutritious farinaceous core. He uses them to prod the ground to discover whether it is firm enough to bear his weight, and with them he attacks and kills his enemies. Many mountain goats, when they accidentally fall from great heights, strike upon their strong and elastic horns, and thus break the force of the blow. In fact, most of the weapons which occur in male animals are used for defence or protection, as well as in their conflicts with other males. The presence of these organs often saves the life of their possessor, and it would therefore seem as if they would be more modified by natural selection than by sexual selection, for natural selection usually means death to the unarmed male, while the result of sexual selection is simply a decreased number of descendants. But natural selection acts upon the female as well as the male, and as the care and protection of the young usually falls to the female mammal, it would seem as if she as well as the male ought to have special weapons of de-

fence. The welfare of the race does not depend upon the number of young which are born, but upon the number which grow up; and if we take two cases, one variety in which the male has special weapons which enable him to drive away his rivals and thus to produce a great number of children, and another variety in which the female has special weapons which enable her to protect her young from enemies, and thus rear them all in safety, it certainly seems as if the modification would be most sure of perpetuation in the second case, and that the second variety should, in time, exterminate the first.

As a matter of fact we do find that the weapons of mammals exist in many cases in the female, but they are most developed and most modified in the male, and it is hard to understand why variations of this kind should not more frequently arise and become hereditary in the female, unless something besides sexual selection determines that males should be more plastic than females.

The modification of the female is certainly quite possible, for there are numbers of cases in all groups of the animal kingdom where the females alone have some peculiar characteristic which is not directly concerned in reproduction.

Thus Darwin says (*Variation*, Vol. I. p. 333): "The tarsi of the front legs are dilated in many male beetles or are furnished with broad cushions of hairs; and in many genera of water-beetles they are armed with a round flat anchor, so that the male may adhere to the slippery body of the female. It is *a much more unusual circumstance* that the females of some water beetles (Dytiscus) have their elytra deeply grooved, and in *Acilius sulcatus* thickly set with hairs, as an aid to the male."

We have seen that the males of many species of crustacea have various parts of their bodies especially modi-

fied for clinging to the female, and we can understand that natural selection will perpetuate modifications of this kind, for the males which adhere most firmly to the females will leave the greatest number of descendants, who will inherit their peculiarity; but the same rule would hold good if certain females were so modified as to afford a good surface for the male to cling to, as we may see from the fact that in a few forms the females are thus modified.

Fritz Müller has described certain species of amphipod crustacea, of the genus Melitu, in which the female does have special hook-like processes for the male to cling to, and cases of this kind are sufficiently numerous to show that when a useful female modification does appear it becomes hereditary. In all cases where the sexes are separated and different from each other, the female undoubtedly might be benefited by peculiar organs as frequently as the male. How then are we to account for the remarkable fact that the cases of male modification of this kind are so very much more numerous than the instances of female modification?

Darwin concludes that we must believe that the male is more variable than the female, and we shall subsequently see that this is so, and the reason for it. Still the female does vary, and vary greatly, and unless there is some reason why female variations should be less apt than male variations to become hereditary, the great preponderance of special male modifications is incomprehensible.

The Male more Eager than the Female.

Darwin attributes this to the greater eagerness of the male. He says (*Sexual Selection*, Vol. I. p. 263): "Throughout the animal kingdom, when the sexes

differ from each other in external appearance, it is the male which, with rare exceptions, has been chiefly modified: for the female still remains more like the young of her own species, and more like the other members of the same group. The cause of this seems to lie in the males of almost all animals having stronger passions than the females."

He points out that it is the males that fight together and display their charms before the females; that among mammals, birds, fishes, reptiles, and batrachians, the male is known to be much more eager than the female; that among insects it is a law that the male seeks the female; that among spiders and crustacea the males are more active and erotic than the females, and that in these latter groups the organs of sense and of locomotion are often more highly developed in the male than in the female. The female, on the other hand, is, with the rarest exceptions, less eager than the male: she is coy, requires to be courted, and may often be seen for a long time endeavoring to escape from the male.

He gives the following explanation of the manner in which the male has been rendered more eager than the female, so that he searches for her and plays the more active part in courtship in so many widely distinct classes of animals:

"It would be no advantage and some loss of power if both sexes were mutually to search for each other; but why should the male almost always be the seeker? With plants, the ovules after fertilization have to be nourished for a time; hence the pollen is necessarily brought to the female organs—being placed on the stigma, through the agency of insects or of the wind, or by the spontaneous movements of the stamens, and with the algæ, etc., by the locomotive power of the antherozooids. With lowly

organized animals permanently affixed to the same spot, and having their sexes separated, the male element is invariably brought to the female; and we can see the reason, for the ova, even if detached before being fertilized and not requiring subsequent nourishment and protection, would be, from their larger relative size, less easily transported than the male element. Hence, plants and many of the lower animals are in this respect analogous. In the case of animals not affixed to the same spot, but enclosed within a shell, with no power of protruding any part of their bodies, and in the case of animals having little power of locomotion, the males must trust the fertilizing element to the risk of at least a short transit through the waters of the sea. It would, therefore, be a great advantage to such animals, as their organization became perfected, if the males, when ready to emit the fertilizing element, were to acquire the habit of approaching the female as closely as possible. The males of various lowly organized animals have thus aboriginally acquired the same habit which would naturally be transmitted to their more highly developed male descendants; and in order that they should become efficient seekers, they would have to be endowed with strong passions. The acquirement of such passions would naturally follow from the more eager males leaving a larger number of offspring than the less eager."

Need for a more Fundamental Explanation.

This is all undoubtedly true, as far as it goes, but it does not cover the whole ground. The sexual passion of the male is undoubtedly stronger, as a rule, than that of the female, and as the existence of the species depends upon the strength of this passion, there will undoubtedly be a selection of the most eager males.

We must recollect, however, that the sexual passion is not the only one upon which the perpetuation of the species depends. The parental feeling or passion is fully as important, and as a rule this is most developed in the female. In the same way that the males which are best fitted for pleasing and commanding the females are naturally selected, those females which are best adapted for protecting, feeding, and educating the young would be picked out from generation to generation. If any hereditary variation should appear which contributed in any way to this end, it would be at least as valuable to the species as an extra ornament or a new color in the male; and there are certainly as many possible ways to improve a female animal as there are to improve a male. If these variations of parts which are confined to the female, or which are of use only or chiefly in this sex, are as apt as the similar parts of a male to give rise to hereditary modifications, we should expect the evolution of new improvements in the female body to keep pace with the improvement of the male body.

We should expect, when allied species are compared, to find that the females differ from each other as much as the males; and that while the males are gradually becoming more and more specialized for conflict and rivalry with other males, and for winning the favor of the females, the females are becoming specialized along another path, for the better care and protection of their young. The fact that we find nothing of the kind; that evolution shows itself especially in the males, while the females remain comparatively stationary, shows that we must search for some other explanation than the one given by Darwin. We are, therefore, compelled to recognize, in the general rule that the male is more modified than the female, the evidence of some cause

more fundamental and general than the great exposure of the male, through the intensity of the sexual passion, to the influence of selection; for the parental instinct is fully as important for the welfare of the race as the sexual instinct, and the former is, as a rule, most developed in the female, just as the latter is greatest in the male, and it might be expected to lead to the selection and modification of females, as the latter passion does to the modification of males.

The Theory of Heredity Furnishes the Only Adequate Explanation.

We must acknowledge that the great body of facts detailed in the beginning of this chapter have no adequate explanation, except on the hypothesis that a part which is present, or functional, or most important in the male alone, is very much more likely than a part which is limited to females in the same way, to give rise to hereditary variations. The facts receive a ready explanation on the hypothesis that there is an especial adaptation for the transmission to the egg of gemmules thrown off by the cells of the male body, while their transmission in the female is not thus provided for, but is due to accident. According to this view we must, in animals where the sexes have long been separated, look to the cells of the male body for the origin of a large proportion of the variations which have gradually been accumulated in the past to give species their present character; and we must regard secondary sexual characters as differing from ordinary specific characteristics, simply in being especially useful to one sex, usually the male, or in being disadvantageous to the other sex, so that natural selection has developed them to a greater degree in one sex than in the other.

It will be seen that the evidence from this source is, as far as it goes, very similar to the evidence from hybrids. A reciprocal cross between two species furnishes a means of analyzing the influence of the two sexes, and of distinguishing, to some slight degree, the effect of each sexual element in heredity. The study of sexual character gives us another means of doing the same thing on a more limited scale.

As each cell of the body may throw off gemmules, there is no way of showing that a variation in a part which is alike in both sexes, is due to the transmission of gemmules from the cells of one parent rather than from those of the other, but the case is different with a part which is more developed in one sex than it is in the other. In this case we should, according to our theory of heredity, expect it to throw off gemmules most frequently in the sex in which it is of most functional importance, and as we suppose that there is an especial arrangement for the transmission to the egg of those gemmules which originate in the male body, we can see that an organ which is most important in the body of the male is much more likely to give rise to hereditary modification than one which is most important, and therefore most prolific of gemmules, in the female body.

The history of secondary sexual characters is, therefore, what our theory of heredity would lead us to expect, and no other explanation which has ever been proposed fully accounts for all the phenomena.

Instances of Female Modification.

We should not expect, however, to find secondary sexual characters exclusively confined to males, but simply more general than they are in females, and as a matter of fact we do meet with many cases where the female has been more modified than the male.

I will now give a few of those which seem to me to be most opposed to my general conclusion.

Female Modification.

In certain species of the amphipod crustacean, genus Melita, the females differ from all other amphipods by having the sexual lamellæ of the penultimate pair of feet produced into hook-like processes, of which the males lay hold with the hands of the first pair. In another amphipod, *Boachyscelus,* the male possesses, like all other amphipods, a pair of posterior antennæ, but they are absent in the female, so that the latter differs more than the male from allied forms. Darwin states that the females of certain water-beetles, as *Dytiscus Acilius* and *Hydroporus,* have their wing-covers grooved or thickly set with hairs or punctured, in order to enable the male to cling to the slippery surface of their hard and polished bodies.

The call duck is a domesticated breed which receives its name from its extraordinary and exceptional loquacity, and as this loquacity is confined to the female, while the male hisses like other ducks, we must regard this as a case of female modification. We know from the statements of Blumenbach and Bechstein that, previously to the year 1813, the great bony protuberances on the skull which characterize the Polish breed of fowls, were confined to the females, although they are now equally developed in both sexes. There can be no doubt that this peculiarity originated in the females, and was subsequently inherited by the males.

Among the Phasmidæ or spectre insects the females alone, in some species, show a most striking resemblance to leaves, while the males show only a rude approximation, and Darwin has pointed out that, as we can

hardly believe that such a resemblance is disadvantageous to the males, we must conclude that the females alone have varied, and that these variations have been preserved and augmented by natural selection for the sake of protection, and have been transmitted to the female offspring alone.

In two species of Birds of Paradise, *Paradisia apoda* and *Paradisia Papuana,* the females differ from each other more than do their respective males; the female of the latter species having the under surface pure white, while the female of *P. apoda* is deep brown beneath.

The males of two species of shrikes (*Oxynotus*) in the islands of Mauritius and Bourbon, differ but little in color, while the females differ much, so that the female of the Bourbon species might at first sight be mistaken for the young of the Mauritius species. In this case there seems to be every reason for believing that the female of the Mauritius species has varied, while the male has remained unmodified.

Semper states (*Animal Life*) on the authority of Dr. Hagen that the females of many species of cave-beetles are blind, while the males have perfect eyes. As we may feel confident that these beetles are descended from ordinary forms, we must regard this as an instance of female modification.

The remarkable shell which is secreted by the large fan-like arms of the paper nautilus (Argonauta) occurs in the females alone, and it probably owes its origin to female modification, although it it not impossible that our recent species may be descended from a form in which the male had a shell.

The most remarkable cases of female modification are those which are presented by polymorphic insects.

Papilio turnus is one of our common yellow butter-

flies, and it is found over almost the whole of temperate North America. In New England and New York the sexes are alike, but south of lat. 42° some of the females are black, and they are so different from the yellow male and the northern yellow female, that they were for a long time regarded as a distinct species, and have received a specific name, *Papilio glaucus.* Between lat. 42° and lat. 37° both forms are found, and Prof. Uhler of Baltimore, has reared the yellow female *Papilio turnus,* and the black one, *P. glaucus,* from the same lot of eggs, but further south only the black female is found, although the male is exactly like that which in New England is associated with the yellow female alone.

Wallace has recorded a number of similar cases among the Malayan *Papilionidæ,* of which *Papilio Memnon* is one of the most striking. In this species there are two kinds of females, one closely resembling the male, and the other differently colored, and furnished with long spatulate tail-like elongations of the hinder wings. These tails are not present on the wings of the male nor on those of the second female, although they are found in both sexes of other species of Papilio, and in some other less specialized genera of the Papilio family. The males, the tailed and the tailless females have all been reared from a single group of eggs, so there is no doubt that they all belong to the same species.

Wallace has given other cases in which the same male form is found associated, in different countries, with their three different female forms.

It is possible, and indeed probable, that in some of these cases certain females have resembled the male, while others have either remained unmodified or else have reverted back to an ancestral form.

Darwin refers to a case of sexual dimorphism which

occurs in several species of the dragon flies of the genus Agrion, in which a certain number of females are of an orange color, and thus differ from the males and ordinary females.

He suggests that this is probably a case of reversion, for in the true Libellulæ, whenever the sexes differ in color, the females are always orange or yellow, so that, supposing Agrion to be descended from some primordial form having the characteristic sexual colors of the typical Libellulæ, it would not be surprising that a tendency to vary in this manner should occur in the females alone.

This explanation seems to apply to several of the recorded cases of female polymorphism, but not to all, and we must acknowledge that in these cases the female shows, in a far greater degree than the male, a tendency to deviate from the primitive form of the species, and to give rise to new race modifications.

We have already called attention to the fact that among the Crustacea there are many cases of male polymorphism, and many cases of the same kind are known among male insects; as well as many cases, besides those I have mentioned, of female polymorphism.

In many of the social insects we have most profound structural modifications, and most complex instincts, which can only have arisen in females; and as allied species of social insects differ from each other in characters which are confined to the females, we must acknowledge that in these forms there is no lack on the part of this sex of a power to give rise to hereditary race modifications.

That facts of this kind present a serious difficulty I cannot deny, but we must recollect that our hypothesis does not demand that the power to transmit variations should be confined exclusively to males, but simply that

it should be much more active in them than it is in the females, and we certainly find that this is the case. I believe that we may, in justice, conclude that, with greater knowledge of the few cases where females give evidence that they have this power to an exceptional degree, the difficulty will disappear, for they are certainly deviations from a general rule, and they must therefore be regarded as special cases, to be studied by themselves. It is interesting to notice that both parthenogenesis and female race-modification are more frequent among the Anthropods than in most other groups of animals, and that parthenogenesis is known to occur in the Lepidoptera and in the social insects, two of the groups where great modifications can be most clearly traced to a female origin. It is not improbable that the power of the egg to develop without fertilization, and its power to store up and transmit gemmules, may be related in some way, so that when the one power is acquired the other is also.

Every one is aware that we meet, in the most diverse groups of animals, with structures and instincts which are confined to the females; such as the brood-chambers of Daphnia, the ovipositor of the ichneumon fly, the sting of the honey bee, the marsupial pouch of the opossum, the nest-building and incubating instincts of birds, or the nursing habit of female mammals. We must bear in mind, however, that in many of these cases a male origin for the successive variations is not out of the question. The fact that the male Hippocampus and not the female has an incubatory pouch, and that mammæ are present in most male mammals, certainly shows the possibility of a male origin for these structures, and as many male birds either share in the work of nest-building and incubating or aid the female in this duty, there

is certainly no difficulty in believing that these instincts have had a male origin.

The remarkable instinct which leads some species of cuckoo and crow blackbirds to lay their eggs in the nests of other species, must have originated in females, and a collection of all the cases which must be explained in the same way would make a formidable list, but the fact would still remain true, that among animals with separate sexes, male modifications are very much more frequent than female modifications, and this is all that our theory requires.

CHAPTER X.

THE EVIDENCE FROM THE INTELLECTUAL DIFFERENCES BETWEEN MEN AND WOMEN.

(This chapter, which was published in the *Popular Science Monthly* for June and July, 1879, under the title, "The Condition of Women from a Zoölogical Point of View," is reprinted here, almost without change.)

ZOÖLOGY is the scientific study of the past history of animal life, for the purpose of understanding its future history. Since man has, in part at least, conscious control of his own destiny, it is of vital importance to human welfare in the future that we should learn, by this comparative study of the past, what are the lines along which progress is to be expected, and what the conditions favorable to this progress, in order that we may use our exceptional powers in harmony with the order of nature.

The study of the growth of civilization shows that human advancement has been accompanied by slow but constant improvement in the condition of women, as compared with men, and that it may be very accurately measured by this standard. Judging from the past, we may be sure that one of the paths for the future progress of the race lies in this improvement, and the position of women must therefore be regarded as a most important social problem. If there is, as I shall try to show, a fundamental and constantly increasing difference between the sexes; if their needs are different, and

if their parts in the intellectual, moral, and social evolution of the race are, like their parts in the reproductive process, complemental, the clear recognition of this difference must form both the foundation and superstructure of all plans for the improvement of women.

If there is this fundamental difference in the sociological influence of the sexes, its origin must be sought in the physiological differences between them, although the subject is now very far removed from the province of ordinary physiology. While we fully recognize the insignificance of the merely animal differences between the sexes, as compared with their intellectual and moral influence, it is none the less true that the origin of the latter is to be found in the former; in the same manner —to use a humble illustration—that the origin of the self-denying, disinterested devotion of a dog to his master is to be found in that self-negation which is necessary in order that a herd of wolves may act in concert under a leader, for the general good.

In order to trace the origin and significance of the differences which attain to such complexity and importance in the human race, we must carry our retrospect back far beyond the beginning of civilization, and trace the growth and meaning of sex in the lower forms of life. In so doing I shall ask attention to several propositions which may not at first appear to have any bearing upon our subject, or any very close relation to each other. I shall then try to show what this relation is, and point out its bearing upon the education of women.

Every organism which is born from an egg or seed is a resultant of the two systems of laws or conditions which may be spoken of abstractly as the law of heredity and the law of variation, or, to use the old teleological terms, each organism is a mean between the principle of adhe-

rence to type and the principle of adaptation to conditions.

That like produces like is universally but never absolutely true. The offspring resembles its parents in all fundamental characteristics. The human child, for instance, resembles its parents in the possession of all the characteristics which distinguish living things from those which are not alive, as well as those which distinguish animals from plants. The chemical, physical, and physiological changes which take place in its body and the histological structure of its tissues are like those of its parents, and its various organs are the same in form and function. All the characteristics which unite it with the other vertebrates, as a member of the subkingdom Vertebrata, are like those of its parents, and also those which place it in the class Mammalia, and in its proper order, family, genus, and species. It also shares with its parents the features or race characteristics of the particular tribe or race to which they belong. If they are Chinese, Indians, or negroes, the child belongs to the same race, and manifests all the slight, superficial peculiarities of form, constitution, and character by which that race is distinguished. Even the individual peculiarities of the parents, intellectual and moral as well as physical, are now known to be hereditary. Since this holds true of any other animal or plant, we must recognize the universality of the law of heredity, but we must not overlook the equally well-established fact that each organism is the resultant of this law and another, the law of variation. The child is like its parents, but not exactly like them. It is not even a compound of characteristics found in one or the other of them, but has individual peculiarities of its own; slight variations which may not have existed in either

parent, or in any more remote ancestor. The slight individual differences are so overshadowed by the much more conspicuous resemblances due to heredity—with which they compare about as the green buds at the tips of the twigs of a large tree compare with the hard wood of the trunk and branches, the growth of previous years —and they are so fluctuating and inconstant, that their importance may easily escape attention. Careful observation shows, however, that every characteristic may vary: those distinctive of the class or order as well as those which mark the species or variety. The variations may manifest themselves in the adult, or at any other period in the life of the individual. Even the eggs have individualities of their own, and among many groups of animals the eggs of the same parent, when placed under precisely similar conditions, may differ in the rate and manner of development. Although most of these individual differences are transient, and disappear within a few generations, there can now be no doubt that those which tend to bring the organism into more perfect harmony with its environment, and are therefore advantageous, may be established as hereditary features, through the action of the law of the survival of the fittest; and it is hardly possible to over-estimate the value of the evidence which paleontology and embryology now furnish to prove that all hereditary characteristics, even the most fundamental, were originally individual variations.

The series of hereditary structures and functions which makes up the life of an organism is constantly being extended by the addition of new features, which, at first mere individual variations, are gradually built into the hereditary life history. In this way newly acquired peculiarities are gradually pushed further and further from what may be called the growing end of the series,

by the addition of newer variations above them. It can also be shown that from time to time the peculiarities at the other end of the series, the oldest hereditary features, are crowded out of the life of the organism, and dropped, so that an animal which is high in the scale of evolution does not repeat, in its own development, all of the early steps through which its most remote ancestors have passed. The series of hereditary characteristics, thus growing at one end and fading away at the other, gradually raises the organism to new and higher stages of specialization, and its evolution by variation and heredity may be compared with the growth of a glacier.

The slight individual differences are represented by the new layers of snow added by the storms to the deposit which fills the valley in which the glacier arises. The snows which are soon blown away are those variations which, being of no use, soon disappear; while the snow which remains in the valley, and is gradually converted into ice, represents those individual differences which are seized upon by natural selection, and gradually rendered hereditary and constant. The long stream of ice stretching down to lower regions, and made up of the snows of thousands of winters, receiving new additions at its upper end, and at the same time melting away at its lower, is no bad representation of the long series of hereditary features, once variations, which form so large a part of every organism. If the glacier were not in motion, but stationary, so that the melting of the oldest portion and the additions to its upper end should gradually carry the body of ice up to higher and higher levels, we should have a very perfect parallel to the evolution of an organism by variation and heredity.

The steps in this progress are embodied in a long series of individuals, each of which is, either immediately

or indirectly, the product of a fertilized egg or seed, through which the laws of heredity and variation act, to bind the separate individuals into a progressive whole. The seeds and eggs with which we are most familiar are highly complicated, and consist of the protoplasmic germ, which is intimately united to a mass of food destined to be converted into protoplasm during development.

The germ with its food forms the yolk of such an egg as that of the bird, and is surrounded by layers of albumen, which are also used as food, and by a complicated series of investing membranes. It originates in a special organ, the ovary, and is incapable of perfect development until it has been fertilized by the male reproductive element. In its earliest stage of growth it is simply one of the cells or histological elements of the ovary, but as it grows it soon becomes very much larger than an ordinary cell, and its protoplasm becomes filled with food material, and the outer layers and walls are added to it. In many animals the external envelopes are wanting, and the egg is simply a very large ovarian cell, filled with food material, and capable of developing, under the influence of the male element, into a new organism. In still other animals the food-yolk is wanting, and the egg is small, and does not differ from an ovarian cell; and in still other animals the ovaries are lacking, and cells may become specialized as ova in various parts of the body.

The series is so complete that we may be certain that we are comparing strictly homologous structures, and we may therefore conclude that the egg is nothing but one of the cells of the body, which may, when acted upon by the male element, develop into a new organism, substantially like its parents, with some of the individual peculiarities of each of them, and also with new peculiarities of its own.

From the necessity for impregnation in most cases, it has been assumed that the essential function of the male element is to quicken the germ, and thus start the process of development. It is true that it does have this function in many cases; but comparative study shows that the egg itself is alive, and does not need quickening, and that this must be regarded as a secondary and derived function of the male element, not the essential and primitive function.

That this is the case is shown by the fact that, while the earlier stages in the developmental process are sufficiently alike in different animals to admit of a comparison between them, the stage at which impregnation takes place is not fixed, but variable. In some cases the ovarian egg remains without change until it is impregnated; and the first step in the developmental process, the disappearance of the germinative vesicle, is the immediate result of the union of the spermatozoa with the ovum. In other cases the germinative vesicle disappears, and the egg then remains inactive until it is impregnated; and this is followed at once by segmentation. In other cases segmentation takes place without impregnation. Other eggs develop still further; and, finally, there are many animals whose unfertilized eggs not only commence but complete the developmental process, and give rise to adults which may in turn produce young in the same way: and this may go on indefinitely, without the intervention of a male. The queen bee is able to lay fertilized or unfertilized eggs, and they are equally alive and capable of development.

These facts show conclusively that the essential function of the male element is not the vitalization of the germ.

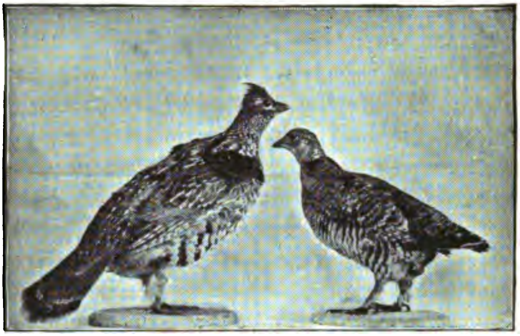
Turning now to another aspect of our subject, we find

that among plants, and among all the lower and simpler groups of animals, new individuals are produced by the various forms of asexual generation, as well as sexually. In certain animals, such as the tunicates, this form of generation is highly specialized, and the stolon from which new individuals are budded off is a highly complex structure, which contains cells or tissues derived from all the essential organs and systems of the parent, and from these the corresponding organs and systems of the new individual are derived. As a rule, however, the process of budding is very simple: a mass of unspecialized cells at some definite point upon the body of the parent animal or plant becoming converted into a new individual, instead of contributing to the further growth of the old. Among the lower animals, such as the hydroids and sponges, the process is still more simple, and cells may become converted into a bud at almost any point upon the body of the parent. That the process of reproduction by budding is not in any way absolutely distinguished from the process of ordinary growth by cell-multiplication, is shown by the fact that an accident may determine which of these processes is to result from the activity of a given cell.

Comparison shows that there is, on the one hand, no essential distinction between ordinary growth and reproduction by budding, and, on the other hand, none except the necessity for impregnation to distinguish asexual from sexual reproduction. All these processes are fundamentally processes of cell-multiplication. As none of the animals with which we are thoroughly familiar reproduce asexually, we are unable to make any very exact comparison of the results of the two processes of reproduction in animals; but among plants such comparison can be made without difficulty, and will be found to show

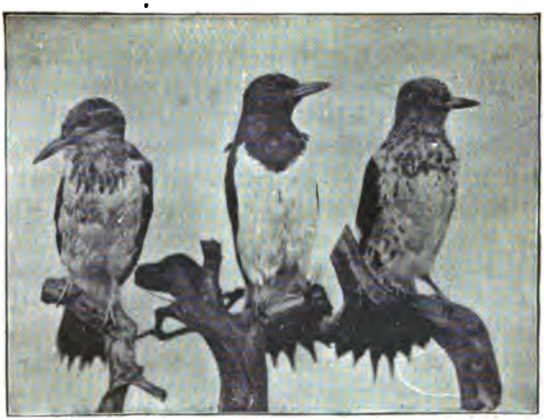
that variation is much more marked and common in plants raised from fertilized seed than in those raised by budding. A marked bud-variation is a very rare occurrence, but in many cases the tendency of plants reared from seeds to differ from the parents is so great that choice varieties are propagated entirely by buds. It is almost hopeless to attempt to propagate a choice variety of grape or strawberry by seeds, as the individuals reared in this way seldom have the valuable qualities of their parents, and, although they may have new qualities of equal or greater value, the chances are of course greatly against this, since the possibility of undesirable variation is much greater than the chance of a desirable sport. There is no difficulty, however, in perpetuating valuable varieties of these plants by asexual reproduction.

Putting together these various propositions—that the evolution of life has been brought about through the combined action of the law of heredity and the law of variation; that in all except the simplest organisms the process of sexual reproduction by ova which have been acted upon by the male element is met with; that the ovum is alive, and capable of development in itself, and that the essential function of the male element is something else than the vitalization of the ovum; that the process of sexual reproduction differs from the process of asexual reproduction only in the occurrence of impregnation, while the result of the former process differs from the result of the latter in its greater variability—we seem warranted in concluding that the ovum is the material medium through which the law of heredity manifests itself, while the male element is the vehicle by which new variations are added. The ovum is the conservative and the male element the progressive or variable factor in the process of evolution of the race as



MALE. FEMALE.

MALE AND FEMALE RUFFED GROUSE.



YOUNG MALE. ADULT MALE. ADULT FEMALE.

ADULT MALE, YOUNG MALE AND ADULT FEMALE OF THE RED HEADED WOODPECKER.

[*From photographs of stuffed specimens in the collection at Druid Hill Park, Baltimore.*]

well as in the reproduction of the individual. The adequate statement of the evidence upon which this generalization rests, or even a full statement of the generalization itself, with its qualifications, would be out of place here, but the facts which have been given seem to be sufficient to warrant its use as one step in our argument in regard to the relations of the sexes. From this as our basis we will now trace the evolution of sex.

Among the lowest organisms, animal and vegetable, multiplication is usually by the various forms of asexual generation, budding or fission, or cell-multiplication—an organism which has by ordinary growth increased in size beyond the limit of exact harmony with its environment, dividing in this way into two, like each other as well as like their parent. In this way the preservation of the established characteristics of the species—heredity—is provided for, but in order that progress should take place, by the preservation of favorable varieties, variation must also be provided for. This is accomplished by the process which is known as conjugation: two protoplasmic organisms approach, come into contact, and a transfusion or mixture of the semi-fluid contents of their bodies takes place. The result of this process is the production of new individuals which, deriving their protoplasm from two parents which are not exactly alike, are themselves different from either of them, and have individual peculiarities which are, it is true, the resultant of the peculiarities of the parents, but which are nevertheless new variations.

In the simplest forms of conjugation the functions of both parents appear to be identical, but in organisms which are a little more specialized we find male and female reproductive bodies, and the offspring is the result of the union of the male element of one individual with

the female element of another; that is, we have true sexual reproduction in its simplest form.

Among the lower animals and most plants both sexes are united in the same individual, but the law of physiological division of labor, the principle that an organ or organism, like a machine, can do some one thing better and with less expenditure of force when it is specially adapted to this one thing than when it is generally adapted for several functions, would lead to the preservation by natural selection of any variations in the direction of a separation of the sexes, and we should therefore expect to find among the higher animals what we actually do find—the restriction of the male function to certain individuals, and the restriction of the female function to others. From this time forward the male is an organism specialized for the production of the variable element in the reproductive process, and the female an organism specialized for the production of the conservative element. We soon meet with structural peculiarities adapted to aid and perfect the performance of these respective functions; and the various organs, habits, and instincts by which, among the higher animals, the rearing of young is provided for, form one of the most interesting chapters of natural science. On *a priori* grounds we should expect a still greater specialization to make its appearance. Since the male organism has for its function the production of the variable reproductive element, and since variations which originate in a male have their perpetuation especially provided for, it would clearly be of advantage that the male organism should acquire a peculiar tendency to vary, and any steps in this direction would accordingly be seized upon by natural selection and perpetuated. The female organism, on the other hand, having for its function the

transmission of the established hereditary features of the species, we should expect the female to gradually acquire a tendency to develop these general characteristics more perfectly than the male. The male organism would thus gradually become the variable organism, as well as the transmitter of variations, and the female organism would become the conservative organism, as well as the originator of the conservative element in reproduction.

The study of the higher forms of life shows that this specialization has actually taken place in many cases, and that, in nearly all cases in which the sexes differ in peculiarities not actually concerned in reproduction, the male has varied more than the female. The amount of variation which any organism has lately undergone may be learned in two ways—by a comparison of allied species, and by a comparison of the adult with the young. In a genus which comprises several species the characteristics which these species have in common are due to heredity from a common ancestor, and are therefore older than features which are confined to any one species. Now, it is a well-known ornithological law that the females of allied species of birds are very much more alike than the males, and that in some cases where the females can hardly be distinguished the males are very conspicuously different—so much so that there is not the least danger of confounding them. Countless examples will present themselves to any one who is at all familiar with birds, and those who are not can at once find ample proof by glancing through any illustrated work on ornithology—Gould's "Humming-Birds," for example.

The greater variability of the male is also shown by a comparison of the adult male and female with the immature birds of both sexes. Since the growing animal tends to recapitulate, during its own development, the

changes through which its ancestors have passed, substantially in the order in which they first appeared, it follows that, in cases where the sexes are unlike, the one which is most different from the young is the one which has varied. Now, it is only necessary to compare the nearly full-grown young of our domestic fowls with the adult cock and hen, to perceive that the adult hen agrees with the young of both sexes in lacking such male characteristics as the highly ornamented tail-feathers, the brilliant plumage, the distended comb, the spurs, and the capacity to crow. Countless similar illustrations might be given to show the great tendency of the male to vary, but the above are sufficient for the purposes of our argument. As both sexes usually retain the more general specific and generic characteristics, and are alike as far as these are concerned, it is a little more difficult to show the conservative constitution of the female than it is to prove the male tendency to vary. Among the Barnacles there are a few species the males and females of which differ remarkably. The female is an ordinary barnacle, with all the peculiarities of the group fully developed, while the male is a small parasite upon the body of the female, and is so different from the female of its own species, and from all ordinary barnacles, that no one would ever recognize, in the adult male, any affinity whatever to its closest allies. All of the hereditary race characteristics are wanting: the limbs, digestive organs, and most of the muscles and nerves have disappeared, as they are not needed by a parasitic animal; and the male is little more than a reproductive organ attached to the body of the female. It is only when the development of the male is studied that we obtain any proof of its specific identity with the female. The young of both sexes are alike, and the developing

male shares with the female the characteristics which unite them to the other barnacles, and which are due to descent from a common form. The female keeps these hereditary characteristics through life, while the male soon loses them entirely.

These facts seem to be sufficient to prove that the specialization which we should expect to find among the higher animals with separate sexes does exist, and that the male organism is especially and peculiarly variable, and the female organism especially and peculiarly conservative.

Leaving this aspect of our subject for the present, let us look at it from a somewhat different point of view. The history of the evolution of life has not only an objective side, but something which may with perfect propriety be spoken of as a subjective aspect. The progress which is shown objectively as greater and greater specialization of structure, and a closer and closer adaptation of the organism to the conditions of the external world, has been well described by Herbert Spencer, as the increasing delicacy, exactness, and scope of the adjustment between internal and external relations. Seen in its subjective aspect, each of the steps in the growth of this adjustment is a recognition of a scientific law, the perception of the permanency of a relation between external phenomena; for science is simply the recognition of the order of nature.

When a Rhizopod discriminates between the contact of a large body and that of a small one, and draws in its pseudopodia and shrinks into as compact a shape as possible in order to escape the danger which the past experience of the race has shown to be related to the former sensation, or when it expands its pseudopodia in order to ingulf and digest the body which has caused

the second sensation, it furnishes proof that its scientific education has begun. Of course I do not intend to say that the order of nature, according to which the Rhizopod adjusts its actions, is consciously apprehended, but simply that it is the experience of the existence of this order which determines the action. Throughout the whole course of the evolution of one of the higher organisms each variation which served to bring about a closer harmony between the organism and its environment, and was accordingly preserved by natural selection, and added on to the series of hereditary structures and functions, was in its subjective aspect the experience of a new external connection, a new step in the recognition of natural law, an advance in scientific knowledge. Human advancement is of course widely different from the slow progress of the lower forms of life, but it is fundamentally the same. Experience is continually spreading over new fields, and bringing about a more wide and exact recognition of the persistent relations of the external world. The scientific laws thus recognized then gradually take the shape of principles or laws of conduct, according to which actions are determined in those cases where experience has shown that they apply. Those laws of conduct which have been long recognized gradually assume the shape of habits or intuitions, according to which conduct is almost unconsciously regulated, and the habit finally becomes established as one of the hereditary characteristics of the race.

We are apt to confine our attention to the subjective side of human advancement, and to neglect the structural side, and at the same time to neglect the subjective side of the evolution of the lower forms of life, and to confine our attention to the structural side, but of

course no one can doubt that a new habit is represented by a new specialization of structure, and is transmitted, like any other peculiarity, by heredity.

If this is so, and if the female organism is the conservative organism, to which is intrusted the keeping of all that has been gained during the past history of the race, it must follow that the female mind is a storehouse filled with the instincts, habits, intuitions, and laws of conduct which have been gained by past experience. The male organism, on the contrary, being the variable organism, the originating element in the process of evolution, the male mind must have the power of extending experience over new fields, and, by comparison and generalisation, of discovering new laws of nature, which are in their turn to become rules of action, and to be added on to the series of past experiences.

Our examination of the origin and significance of the physiological differences between the sexes, and of the parts which they have taken in the progress of the past, would therefore lead us to expect certain profound and fundamental psychological differences, having the same importance; and it will be interesting to examine what these intellectual and ethical differences are, and how far experience and the common consent of mankind accord with the demands of our hypothesis.

If, as we suppose, the especial and peculiar function of the male mind is the expansion of our circle of experience; the more exact apprehension of all our relations to the external world; the discovery of the laws of thought, of society, of physiology, and of the material universe, and of the bearing of these laws upon individual conduct—it will follow that men must excel women in their power to discover the manner in which a new external relation shall be met and provided for by a new

internal adjustment. In a case where our instincts, intuitions, feelings, or past experiences furnish no guide to conduct, the judgment of a man as to the proper course of action will be of more value than the judgment of a woman.

On the other hand, only a very small proportion of our actions are directed to new conditions; experience has already determined the proper conduct in all the circumstances upon which our preservation and well-being most directly depend; and action in these circumstances does not demand comparison and judgment, while it must usually be so prompt as to forbid deliberation or thought. The power of quick and proper action in the innumerable exigencies of ordinary life, independent of reflection, is at least equally important with the power to extend our field of rational action.

By the former power we hold on to what has already been gained, while the latter power enables us to increase our advantage in the struggle for existence, and to widen our control over the laws of nature. Psychological variation is the result of the latter power, psychological heredity the result of the former, and psychological evolution and human progress the result of their combined action.

If the female mind is especially rich in the fruit of this past experience, we should expect women to excel men in the promptness and accuracy with which the conduct of ordinary life is decided, and in the range of circumstances over which this power of rational action without reflection extends; that is, we should expect men to excel in judgment, women in common sense.

This important and fundamental difference between the male intellect and the female must have a very great influence in determining the occupations or professions

in which each sex is most likely to succeed when brought into fair competition with the other sex.

The originating or progressive power of the male mind is shown in its highest forms by the ability to pursue original trains of abstract thought, to reach the great generalizations of science, and to give rise to the new creations of poetry and art. The capacity for work of this character is of course very exceptional among men; and, although history shows that it is almost exclusively confined to men, it must not enter into our conception of the ordinary male mind. The same power of originating and of generalizing from new experiences is possessed, in a lesser degree, however, by ordinary men, and gives them an especial fitness for and an advantage over women in those trades, professions, and occupations where competition is closest, and where marked success depends upon the union of the knowledge and skill shared by competitors, to the inventiveness or originality necessary to gain the advantage over them.

Women, on the other hand, would seem to be better fitted for those occupations where ready tact and versatility are of more importance than the narrow technical skill which comes from apprenticeship or training, and where success does not involve competition with rivals.

The adequate examination of this aspect of our subject would furnish material for a treatise, and it is out of place here, as all that is necessary for the purposes of our argument at present is to point out the difference, and to show that it is the necessary consequence of our view of the manner in which sex has been evolved: that it is not due to the subjection of one sex by the other, but is the means by which the progress of the race is to be accomplished.

Turning now to another part of our subject, and bear-

ing in mind the fact that by far the greater part of the external relations to which our actions are adjusted, and to which it is necessary that they should conform, in order to secure our preservation, safety, and welfare, are fixed and definite, and have been substantially unchanged for almost, if not quite, the whole period of human development, we see at once that, if the female mind is especially rich in the past experiences of the race, so far as these have resulted in laws of conduct, it follows that, since these experiences have been the same for all members of the race, there must be a greater uniformity in female character than in male character. As this statement is very abstract, I will try to put it in a less general form:

Experience of the order of events has shown that under certain circumstances, of frequent occurrence, certain conduct is proper and conducive to welfare, while its opposite is hurtful.

This experience being constantly repeated, the tendency to do the proper thing when the circumstances occur gradually takes the shape of an instinct, intuition, habit, or law of duty. Henceforward, all persons who have the impulse which has thus been formed will act in the same way when the circumstances arise, but two persons who have not the impulse will follow their individual judgments, and may or may not act alike.

As the female mind is characterized by the possession of these impulses, it is plain that it must be much more easy for one average woman to predict what another average woman will do, or feel, or think, or say in any given case, than for one average man to predict in the same way of another average man.

We may carry this line of thought a little further. Since male minds have the element of originality, male characters differ among themselves; but, since all are

members of the same species, fundamental similarity must underlie this individual diversity, and this fundamental similarity must subsist between female and male characters also. The average female character will therefore have more resemblance to two or more male characters than these latter will have to each other, and accordingly, in all cases where relationship or education has not led two men into the same way of looking at things, a woman will be better able than either of them to foresee the conduct of the other under given circumstances, and of course the advantage of a woman over a man in understanding the conduct of a woman will be still greater.

Since, on the whole, the differences between male characters are slight when compared with their resemblances, and since the points of resemblance are also points of resemblance to women, we should expect that, although the power of women to foresee male conduct is greater than the power of men to foresee female conduct, the superiority is not so marked as in the other three cases. This superiority of women in predicting conduct will be shown by their possession, to a much greater degree than men, of the power to influence or persuade as distinguished from the power to convince or move by arguments; for to convince is to innovate and place matters in a new light, but the secret of influence is a vivid appreciation of the established motives and incentives to conduct.

The relative power of persuasion of the two sexes, then, may be tabulated as follows:

The power of	To foresee the conduct of or to influence	Is greater than the power of	To foresee the conduct of or to influence
Women	Women	Men	Men
Women	Women	Men	Women
Women	Men	Men	Men
Women	Men	Men	Women

It seems hardly necessary to point out the fact that in cases where sex is a motive and influences the conduct directly, the law stated in this table does not hold.

According to our hypothesis, the first line of the table should give the arrangement in which the difference is greatest. In the next line the difference is less; still less in the next; and least of all in the last case. In all cases, however, the superiority of women in this respect should be very marked.

Since our feelings are necessarily much more numerous than our judgments, we should expect to find it much more easy to persuade either a man or a woman than to convince; but, if our theory is correct, the advantage of influence over argument should be much greater when a woman is to be moved than when the effort is directed to a man.

Another difference between the sexes will at once be seen to follow from the above parallel. Since male character has the variable element, and may vary toward either good or bad, it follows that the ideally perfect male character will be more hard to define and more seldom realized than the ideal female character. It is difficult to prove such a statement as this, for the sentiments upon which individual opinion of the subject is based hardly admit of exact statement, but that there is an accepted standard of female excellence, and that the women who realize it are not rare exceptions, can, I think, be shown by the study of female character as depicted by dramatists, novelists and poets. An appeal to this test is unfavorable to our hypothesis, for characters are selected for novels or poems on account of their originality; but I think that any one who will review Shakespeare, Thackeray or George Eliot with the subject in mind, and who will compare the more important female characters, will find that they might be trans-

posed from one novel or play to another with much less violence than would attend the transposition of the male characters.

It is hardly necessary to call attention to the obvious fact that our conclusions have a strong leaning to the conservative or old-fashioned view of the subject—to what many will call the "male" view of women. The positions which women already occupy in society and the duties which they perform are, in the main, what they should be if our view is correct; and any attempt to improve the condition of women by ignoring or obliterating the intellectual differences between them and men must result in disaster to the race, and the obstruction of that progress and improvement which the history of the past shows to be in store for both men and women in the future. So far as human life in this world is concerned there can be no improvement which is not accomplished in accordance with the laws of nature; and, if it is a natural law that the parts which the sexes perform in the natural evolution of the race are complemental to each other, we cannot hope to accomplish anything by working in opposition to the natural method. We may, however, do much to hasten advancement by recognizing and working in accordance with this method.

It is no more than just, too, to point out that the peculiar bodily organization and physiological functions of woman have nothing to do with our conclusion. If the perpetuation of the human race were as simple as that of the starfish, where the demands made upon the female organism during reproduction are no greater than those made upon the male, the mind of woman would still be the organ of intellectual heredity, and the mind of man the organ of intellectual variation.

Up to this point I have simply indicated some of the

differences between the sexes which the study of the evolution of organisms would lead us to expect. I shall now quote a few extracts from authors whose writings upon the position of women are accepted as valuable contributions to our knowledge of the subject, in order to show that they have recognized the existence of the very differences which we have been led, by theoretical reasoning, to expect.

Mill's essay on "The Subjection of Woman" must be regarded as the most important contribution to the discussion of the relative positions of the sexes as relating to future progress; and it is interesting to note that, while he holds that the existing differences are not natural, but are due to the subjection of one sex by the other, he fully recognizes certain profound and characteristic differences, which are precisely in accordance with the present view of their origin and purpose. Mill's evidence as to important differences between the sexes is of the greatest value, both on account of the weight of his opinion in itself, and on account of his being in this case an unwilling witness. He says: "Looking at women as they are known in experience, it may be said of them, with more truth than belongs to most generalizations on the subject, that the general bent of their talents is toward the practical. This statement is conformable to all the public history of women in the present and in the past. It is no less borne out by common and daily experience. Let us consider the special nature of the mental capacities most characteristic of a woman of talent. They are all of a kind which fits them for practice, and makes them tend toward it. What is meant by a woman's capacity of intuitive perception? It means a rapid and correct insight into present facts. It has nothing to do with general principles.

Nobody ever perceived a scientific law of nature by intuition, or arrived at a general rule of duty or prudence by it. These are results of slow and careful collection and comparison of experience; and neither the men nor the women of intuition usually shine in this department, unless, indeed, the experience is such as they can acquire by themselves. . . . To discover general principles belongs to the speculative faculty; to discern and discriminate the particular cases in which they are or are not applicable constitute practical talent; and for this women, as they now are, have a peculiar aptitude." It is only necessary to change two or three words in this last sentence in order to show its complete agreement with the demands of our theory. Its meaning will not be altered by the following reading, which serves to bring out more clearly its implications: To discover general principles belongs to the progressive aspect of the mind, which is most strongly developed in men; to preserve and apply the general principles which are already established belong to the conservative side of the mind, and for this women, as they have been made by the evolution of the race, have and should have a peculiar aptitude. Mill continues as follows: "I admit that there can be no good practice without principles, and that the predominant place which quickness of observation holds among a woman's faculties makes her particularly apt to build over-hasty generalizations upon her own observation, though at the same time no less ready in rectifying these generalizations as her observation takes a wider range. But the corrective to this defect is access to the experience of the human race; general knowledge—exactly the thing which education can best supply."

This sentence, when viewed in connection with our present theory of the relations of the sexes, gives the key

to the question of female education—for that form of education which supplies the general knowledge which is so important for the correct application of principles to special cases is culture, as distinguished from the technical training which looks to the discovery of new laws.

The next passage which I shall quote is of the greatest importance, for, founded as Mill's autobiography and numerous passages in his various works tell us it is, upon the personal experience of his life, it contains the germ of the idea which, if fully investigated, might have led him to entirely remodel his essay upon women; the idea that the sexes do not naturally stand in the relation of superior and inferior, nor in that of independent equals, but are the complemental parts of a compound whole. He says: "This gravitation of women's minds to the present, to the real, to actual fact, while in its exclusiveness it is a source of errors, is also a most useful counteractive of the contrary error. The principal and most characteristic aberration of speculative minds, as such, consists precisely in the deficiency of this lively perception and ever-present sense of objective fact. . . . Hardly anything can be of greater value to a man of theory and speculation, who employs himself, not in collecting materials of knowledge by observation, but in working them up by processes of thought into comprehensive truths of science and laws of conduct, than to carry on his speculations in the companionship, and under the criticism, of a really superior woman. There is nothing comparable to it for keeping his thoughts within the limits of real things, and the actual facts of nature. Women's thoughts are thus as useful in giving reality to those of thinking men as men's thoughts in giving width and largeness to those of women." Here we have a clear recognition of the law that width and largeness, mental

growth, originate in the male, and are then preserved by women, and the context leaves no room to doubt that the "really superior woman" which filled the author's memory at the time this passage was written, was a woman in whom this feminine characteristic was well developed; that she was a woman filled with the fruits of human experience; and it is a little strange that he fails to see that the relation with which, for a man of speculation, there is nothing comparable, may have a wider value, and be of the greatest importance to humanity as a whole.

The next passage which I shall quote is still more to the point. He says: "Let us now consider another of the admitted superiorities of clever women, greater quickness of apprehension. Is this not pre-eminently a quality which fits a person for practice? In action everything depends upon deciding promptly. In speculation nothing does. A mere thinker can wait, can take time to consider, can collect additional evidence; he is not obliged to complete his philosophy at once lest the opportunity should go by. The power of drawing the best conclusion possible from insufficient data is not, indeed, useless in philosophy; the construction of a provisional hypothesis consistent with all known facts is often the needful basis for further inquiry. But this faculty is rather serviceable in philosophy than the main qualification for it; and for the auxiliary as well as for the main question the philosopher can allow himself any time he pleases. He is in no need of doing rapidly what he does; what he rather needs is patience to work on slowly until imperfect lights have become perfect, and a conjecture has ripened into a theorem. For those, on the contrary, whose business is with the fugitive and perishable—with individual facts, not kinds of facts—rapidity of thought

is a qualification next only in importance to the power of thought itself. He who has not his faculties under immediate command in the contingencies of action might as well not have them at all. He may be fit to criticise, but he is not fit to act. Now it is in this that women, and the men who are most like women, confessedly excel. The other sort of man, however pre-eminent may be his faculties, arrives slowly at complete command of them; rapidity of judgment and promptitude of judicious action, even in the things he knows best, are the gradual and late result of strenuous effort grown into habit."

I have quoted these passages from Mill at length, as they give a very clear although somewhat narrow statement, by the strongest advocate of the fundamental likeness of the sexes, of what I take to be the most important psychological difference between them.

According to Mill—and I think that universal experience will justify his view—the highest type of woman is distinguished by her power of intuition, by her concrete acquaintance with the laws and principles which have been established by experience and generalization, by a constitutional knowledge of these laws which amounts to habit, so that she is able to recognize in actual practical life the action which is proper in any given case, without the necessity for a slow process of comparison and thought; by that immediate command of the faculties which is necessary for action.

This power of correctly and promptly applying the established scientific laws, which are the result of all the experience of the past, to the actions of ordinary practical life, is common sense, as distinguished from originality.

The highest type of male intelligence, on the other hand, is distinguished by the power to abstract and com-

pare, and by a slow process of thought to reach new generalizations and laws, and to see these in their abstract and ideal form, freed from all the complications of their concrete manifestations. To this power is often joined a woful and disastrous lack of common sense, or power of prompt and proper decision and action in special cases.

Lecky, in his "History of European Morals," gives an excellent summary of the most marked differences between the male mind and the female; and, although we do not agree with him in thinking that a departure from the male type is in all cases to be regarded as inferiority, we cannot fail to note how exactly his account agrees with the demands of our hypothesis.

He says: "Intellectually a certain inferiority of the female sex can hardly be denied when we remember how almost exclusively the foremost places in every department of science, literature, and art have been occupied by men; how infinitesimally small is the number of women who have shown in any form the very highest order of genius; how many of the greatest men have achieved their greatness in defiance of the most adverse circumstances, and how completely women have failed in obtaining the first position, even in music and painting, for the cultivation of which their circumstances would appear most propitious. It is as impossible to find a female Raphael or a female Handel as a female Shakespeare or a female Newton. Women are intellectually more desultory and volatile than men; they are more occupied with practical instances than with general principles; they judge rather by intuitive perception than by deliberate reasoning or past experience. They are, however, usually superior to men in nimbleness and rapidity of thought, and in the gift of tact, the power of seizing rapidly and faithfully the finer impulses of feeling, and

they have therefore often attained very great eminence as conversationalists, as actresses, and as novelists. In the ethics of intellect they are decidedly inferior. Women very rarely love truth, though they love passionately what they call 'the truth,' or opinions they have received from others. They are little capable of impartiality or of doubt; their thinking is chiefly a mode of feeling; though very generous in their acts, they are rarely generous in their opinions, and their leaning is naturally to the side of restriction. They persuade rather than convince, and value belief rather as a source of consolation than as a faithful expression of the reality of things. They are less capable than men of distinguishing the personal character of an opponent from the opinions he maintains. Their affections are concentrated rather on leaders than on causes, and if they care for a great cause it is generally because it is represented by a great man, or connected with some one whom they love. In politics their enthusiasm is more naturally loyalty than patriotism. In benevolence they excel in charity rather than in philanthropy." While I cannot believe that Lecky's statement is entirely unprejudiced, I think no one will deny that the views which I have quoted agree in the main with those which have gained general acceptance in the past. At the present time, however, there is a growing tendency to regard the relations of the sexes as due in great part to male selfishness; and while the substantial correctness of our view of the differences between the male and the female character is acknowledged, its origin is attributed to the "subjection" of women by men. In this paper I have attempted to present reasons, which I believe are new, for regarding the differences as natural and of the greatest importance to the race.

Those who acknowledge the weight of my argument, as applied to evolution in the past, may, however, question its applicability to the human evolution of the future. It may fairly be urged that while we grant that the course of evolution from the lower forms of life up to rational man has been by the slow process of variation and heredity, we have now passed into a new order of things, and the great advances of the human race have been and now are brought about by the much more rapid and totally dissimilar process of intelligent education. It may be urged that heredity does very little more for the civilized than for the savage child, and that the wide difference between the savage and the civilized adult is mainly the result of the training and instruction of the individual; that it has not been brought about by the destruction of those children whose congenital share in the results of the intellectual advancement of the race is most scanty. It may be urged that, since man has reached a point where progress is almost entirely intellectual, and depends upon his own efforts, he is free from the laws by which development up to that point was reached.

We are not concerned at present with the question how far progress might be accelerated by intelligent selection, and we may therefore conditionally accept the view that future progress, for some time to come at any rate, must depend almost entirely upon education; but, far from holding that this conclusion will allow us to ignore or obliterate the differences between the male and the female intellect, I believe that the full significance of these differences can be appreciated only in their relation to higher education. The scope of the present paper will only allow the space for an outline sketch of the reasons for this belief. As the field of human knowl-

edge widens in all directions, as society becomes more complex, and as the points of contact between man and his inorganic environment multiply, the amount of general education which each individual must receive before he is in a position to hold his own, and to guide himself rationally in all the emergencies of life, and to enjoy his share of the benefits which our intellectual advancement has placed within his reach, increases in a geometrical progression, and the amount of time demanded for general liberal education increases in the same ratio. Meanwhile the amount of special preliminary training which must be undergone in order to fit a person for new and original work in any department of knowledge or art increases at the same rate, and makes greater and greater inroads upon the time which is needed for general education. At present the most important, delicate, and complicated of educational problems, the problem which each individual must meet and decide upon, and the problem which engrosses most of the thought of educational bodies, is where to draw the line between general culture and practical or technical training.

Culture in its widest sense is, I take it, thorough acquaintance with all the old and new results of intellectual activity in all departments of knowledge, so far as they conduce to welfare, to correct living, and to rational conduct; that is, culture is to the intellectual man what heredity has been to the physical man. Culture is concerned only with results, not with demonstrations, and it does not look to new advances; while technical training is concerned with methods and proofs; and it values the results of the methods and investigations of the past only as they contribute to new advances. Technical training looks to progress in some one definite line, one radius of the growing circle of the domain of

human intelligence, and ignores the rest of the circumference. It is to the intellectual man what variation is to the physical man. By culture we hold our own, and by technical training we advance to higher levels. Both are equally important to human welfare, and the great problem of the future is how to secure each to the greatest degree without sacrificing the other. The analogy of the rest of the organic world would seem to indicate that this is to be accomplished by "division of labor." If the female mind has gained during its evolution an especial aptness for acquiring and applying the results of past progress, by an empirical method and without the necessity for studying proofs and reasons, it would seem especially fitted for culture, as distinct from training, while the male mind is best fitted for education by that process of inductive training by demonstration and experiment which leads to new advances. The methods employed in the general instruction of young men and young women should not therefore be identical. With the one the field may be very wide and the methods empirical, and with the other the range more narrow and the methods more strictly logical. In this way each type of mind will be developed in the manner for which it has an especial fitness; and we have the strongest grounds for the belief that this method would also gradually result in the extension of that congenital acquaintance with nature which is the common stock of the race, and would thus leave more time for the special training of those minds which are by nature best fitted to receive it. It is unavoidable that a bald outline of a view which has such wide implications should afford many openings for serious criticism; but the present article does not admit of the expansion of the idea, even if its detailed examination could be fairly included in the province of

biology. Having traced the origin and significance of sex from its lowest manifestations to a point where it becomes purely intellectual, the biologist may fairly leave the subject in the hands of the psychologist.

When this chapter was printed, several years ago, I was told by several teachers of great experience in the education of both boys and girls that their observations showed no constant difference in the intellectual powers of the two sexes. They therefore disputed the accuracy of my view.

Taking the chapter alone, this is, no doubt, a fair criticism; but I believe that any reader who will examine the subject in connection with the other chapters of this book, as a part of the whole, and not as an isolated essay, will perceive that we should not expect the intellectual differences between men and women to be so well marked and conspicuous during childhood as they become after maturity is reached.

The subject is such a fruitful source of controversy that I can hardly hope to escape adverse criticism, and I can only say that I have not approached it in a spirit of controversy, and shall gladly welcome any discussion which leads to the discovery of truth.

The acceptance of my view should put an end to all discussion as to the relative intellectual rank of men and women; for if the two sexes contribute in different ways to the welfare of the race, and fill equally important but dissimilar places, there can be no question as to relative superiority or inferiority.

CHAPTER XI.

THE THEORY OF HEREDITY CONSIDERED AS SUPPLEMENTARY TO THE THEORY OF NATURAL SELECTION.

Darwin believes that variations are purely fortuitous—Natural selection cannot give rise to permanent race modifications unless many individuals vary in nearly the same way, at about the same time—The chances against this are very great if variations are fortuitous—Argument from North British Review—Darwin acknowledges the great weight of this objection—It is removed by the theory of heredity—The co-ordinated modification of complicated organs—The time demanded by Darwin practically infinite—Murphy's argument from the complexity of the eye—Herbert Spencer's illustration—Our theory removes this difficulty—Mr. Conn's objection—Saltatory evolution—Evidence that it occurs—Spike-horn buck—Ancon and Mauchamp sheep—Black-shouldered peacock—The theory of heredity accounts for saltatory evolution—Parallel variation—Evidence of its occurrence—Evolution of the medusæ—General and special Homologies.

According to Darwin's view, variations, though determined by definite causes (for the most part unknown), are, so far as their usefulness to the organism goes, fortuitous, and he makes use of the following illustration to explain his conception:

"I have spoken of selection as the paramount power, yet its action absolutely depends upon what we in our ignorance call spontaneous or accidental variability. Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental, yet the shape of each has been determined by the force of gravity, the

nature of the rock, and the slope of the precipice—events and circumstances all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up by the power of selection, whether this be natural or artificial selection."

"If our architect succeeded in rearing a noble edifice, using the rough wedge-shaped fragments for the arches, the longer stones for the lintels, and so forth, we should admire his skill even in a higher degree than if he had used stones shaped for the purpose. So it is with selection, whether applied by man or by nature; for though variability is indisputably necessary, yet when we look at some highly complex and excellently adapted organism, variability sinks to a quite subordinate position in comparison with selection, in the same manner as the shape of each fragment used by our supposed architect is unimportant in comparison with his skill" (*Variation*, xxi. p. 301).

It is quite possible that Darwin may be right in attributing the modification and adaptation of organisms almost entirely to the influence of natural selection, and, at the same time, wrong in his belief that the variations are fortuitous. Several critics have pointed out that if it is true that variations have no relation whatever to the needs of the organism, there are grave difficulties in the way of natural selection; but the theory rests upon too firm a basis to be easily set aside, and these objections have hardly received the attention which they fairly deserve, for those authors who have pointed them out have, at the same time, attacked the general theory in a hostile spirit without proposing any-

thing to take its place. This has not prevented Darwin himself from perceiving the weight of the criticism, but it has certainly caused the objections to be ignored or overlooked by other less candid writers.

Natural selection cannot act unless many individual vary together.

One of the most serious objections to Darwin's theory is based upon the fact that while natural selection requires that great numbers of individuals shall vary in essentially the same way at nearly the same time, the chance against this, if variations are fortuitous in Darwin's sense, is great beyond all computation.

In 1864 the writer of what Darwin terms "an able and valuable article" in the *North British Review*, called attention to the fact that, according to the law of chances, slight variations, however useful, will tend to be obliterated, instead of perpetuated, by natural selection, unless they simultaneously appear in a great number of individuals. Unless we can show that the causes of variability act in such a way as to affect many individuals at the same time, and cause the same part to vary in all of them, we must regard this as a very serious objection to the theory of natural selection, and Darwin himself acknowledges (*Origin of Species*, p. 72) that the justice of this objection cannot be disputed. He admits in the later editions of the *Origin of Species*, p. 71, that until reading the able and valuable article in the *North British Review*, he did not appreciate how rarely single variations, whether slight or strongly marked, would be perpetuated.

The reviewer points out that it is difficult to see how a species can be changed by the survival of the descendants of a few individuals which possess some favorable

variation, even when the variation is of the very greatest advantage to its possessor; and that this difficulty is very much greater when as must usually be the case, the advantage gained is very slight.

He says: "The advantage, whatever it may be, is utterly out-balanced by numerical inferiority. A million creatures are born; ten thousand survive to produce offspring. One of the million has twice as good a chance as any other of surviving; but the chances are fifty to one against the gifted individual being one of the hundred survivors. No doubt the chances are twice as great against any one other individual, but this does not prevent their being enormously in favor of *some* average individual. However slight the advantage may be, if it is shared by half the individuals produced, it will probably be present in at least fifty-one of the survivors, and in a larger proportion of their offspring; but the chances are against the preservation of any one 'sport' (*i.e.*, sudden marked variation) in a numerous tribe. The vague use of an imperfectly understood doctrine of chance has led Darwinian supporters, first, to confuse the two cases above distinguished; and, secondly, to imagine that a very slight balance in favor of some individual sport must tend to its perpetuation. All that can be said is that in the above example the favored sport would be preserved once in fifty times. Let us consider what will be its influence on the main stock when preserved. It will breed and have a progeny of say 100; now this progeny will, on the whole, be intermediate between the average individual and the sport. The odds in favor of one of this generation of the new breed will be, say, one and a half to one as compared with the average individual; the odds in their favor will, therefore, be less than that of their parents; but, owing to their greater number, the chances

are that about one and a half of them would survive. Unless these breed together, a most improbable event, their progeny would again approach the average individual; there would be 150 of them, and their superiority would be, say, in the ratio of one and a quarter to one; the probability would now be that nearly two of them would survive and have 200 children with an eighth superiority. Rather more than two of these would survive, but the superiority would again dwindle, until after a few generations it would no longer be observed, and would count for no more in the struggle for life than any of the hundred trifling advantages which occur in the ordinary organs. An illustration will bring this conception home. Suppose a white man to have been wrecked on an island inhabited by negroes, and to have established himself in friendly relations with a powerful tribe, whose customs he has learned. Suppose him to possess the physical strength, energy and ability of a dominant white race, and let the food and climate of the island suit his constitution; grant him every advantage which we can conceive a white to possess over the native; concede that in the struggle for existence his chance of a long life will be much superior to that of the native chiefs; yet from all these admissions there does not follow the conclusion that, after a limited or unlimited number of generations, the inhabitants of the island will be white. Our shipwrecked hero would probably become king; he would kill a great many blacks in the struggle for existence; he would have a great many wives and children. In the first generation there will be some dozens of intelligent young mulattoes, much superior in average intelligence to the negroes. We might expect the throne for some generations to be occupied by a more or less yellow king; but

can any one believe that the whole island will gradually acquire a white or even a yellow population?

"Darwin says that in the struggle for life a grain may turn the balance in favor of a given structure, which will then be preserved. But one of the weights in the scale of nature is due to the number of a given tribe. Let there be 7000 A's and 7000 B's, representing two varieties of a given animal, and let all the B's, in virtue of a slight difference of structure, have the better chance of life by a $\frac{1}{1000}$ part. We must allow that there is a slight probability that the descendants of B will supplant the descendants of A; but let there be only 7001 A's against 7000 B's at first, and the chances are once more equal, while if there be 7002 A's to start, the odds would be laid on the A's. True, they stand a greater chance of being killed, but then they can better afford to be killed. The grain will only turn the scales when these are very nicely balanced, and an advantage in numbers counts for weight, even as an advantage in structure. As the numbers of the favored variety diminish, so must its relative advantages increase, if the chance of its existence is to surpass the chance of its extinction, until hardly any conceivable advantage would enable the descendants of a single pair to exterminate the descendants of many thousands, if they and their descendants are supposed to breed freely with the inferior variety, and so gradually lose their ascendancy."

Darwin acknowledges that the justice of these remarks cannot be disputed, and there is no escape from the conclusion that if variations do not appear simultaneously in a great number of individuals, the theory of natural selection fails to explain the origin of species. But the theory itself is so firmly estabished by other

facts, that the logical conclusion seems to be, not that natural selection is at fault, but that Darwin's opinion, that variations are fortuitous, is an error.

According to our view of the cause of variation, it is plain that a change in the environment, affecting many individuals of a species in the same way, will cause, in succeeding generations, variation of the same cells in all or nearly all of them. It is also clear that since a change in one cell of an organism will disturb the harmonious adjustment of all adjacent or related cells, any variation which makes its appearance will become more marked instead of being obliterated, in the offspring of successive generations.

I think it is clear, without further discussion, that our theory of heredity entirely does away with this very serious difficulty, and furnishes a firmer basis for the theory of natural selection. It is also clear that this cannot be said of the Pangenesis hypothesis, or of any other hypothesis which has been proposed.

The Formation of Complicated Organs by the Natural Selection of Fortuitous Variations demands Unlimited Time.

There is another objection of nearly the same character, which must have struck every thinker with more or less force. How are the various organs of a highly complicated organism, or the various structures which enter into the formation of a complicated organ, kept in harmonious adjustment to each other by the selection of variations which are, in Darwin's sense, fortuitous? It is plain that, as soon as one part has varied in any direction, the harmonious adjustment of related parts will be disturbed, and that they too must vary correspondingly in order to restore the proper tone to the whole, and it is equally clear that even a slight change in a compli-

cated organ will thus, if the various modifications are really fortuitous, require a very great number of generations to supply the necessary variations.

There does not seem to be any logical ground for doubting that any of the adaptations of nature *might have been* produced by the natural selection, from an indefinite number of fortuitous variations, of those which happened to be favorable; but in the case of any complex adaptation, an indefinite and almost infinite period of time would be required.

Darwin says (*Origin of Species*, p. 143) that reason tells us that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further the eye ever varies, and these variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changed conditions of life, then the difficulty of believing that a perfect and complex eye *could be formed* by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory. Before we can accept as possible this view of the evolution of the eye "we must suppose each new state of the instrument to be multiplied by the million; each to be preserved until a better one is produced, and then the old ones to be all destroyed. . . . Let this process go on for millions of years; and during each year on millions of individuals of many kinds; and may we not believe that a living optical instrument *might* thus be formed as superior to one of glass as the works of the Creator are to those of man?"

To show that complex adaptations *might have been* produced by the selection of fortuitous variations is by no means to prove that they *have* thus been produced, and we may well doubt whether life has existed long

enough upon earth, to allow all the harmonious adjustments of living things to be slowly perfected in this way.

The vast number of changes which must be co-ordinated in order to produce any considerable modification of one of the higher animals, and the length of time which must be necessary if the successive steps are purely fortuitous, are points which must have attracted the notice of every one who has read the "Origin of Species." The difficulty is obvious, and it has been noticed by many writers, but Murphy, in his discussion of the evolution of the vertebrate eye (*Habit and Intelligence*, p. 319), has stated it with great force. He says: "The higher the organization, whether of an entire organism or of a single organ, the greater is the number of the parts that co-operate, and the more perfect is their co-operation; and consequently the more necessity there is for corresponding variations to take place in all the co-operating parts at once, and the more useless will be any variation whatever unless it is accompanied by corresponding variations in the co-operating parts; while it is obvious that the greater the number of variations which are needed in order to effect an improvement, the less will be the probability of their all occurring at once. It is no reply to this to say, what no doubt is abstractly true, that whatever is possible becomes probable, if only time enough is allowed. There are improbabilities so great that the common-sense of mankind treats them as impossibilities. It is not, for instance, in the strictest sense of the word, impossible that a poem and a mathematical proposition should be obtained by the process of shaking letters out of a box; but it is improbable to a degree that cannot be distinguished from impossibility; and the improbability of obtaining an improvement in an organ by means of several spontaneous variations, all occurring together, is an improbability of the same

kind. If we suppose that any single variation occurs on the average once in m times, the probability of that variation occurring in any individual will be $\frac{1}{m}$; and suppose that x variations must concur in order to make an improvement, then the probability of the necessary variations all occurring together will be $\frac{1}{m^x}$. Now suppose, what I think a moderate proposition, that the value of m is 1000, and the value of x is 10, then $\frac{1}{m^x} = \frac{1}{1000^{10}}$ 30 $= \frac{1}{10^{30}}$. A number about ten thousand times as great as the number of waves of light that have fallen on the earth since historical time began. And it is to be further observed that no improvement will give its possessor a certainty of surviving and leaving offspring, but only an extra chance, the value of which it is quite impossible to estimate."

No one can be more firmly convinced of the great potency of natural selection than I am, but I am sure every one will feel that the problem of the origin of species would be greatly simplified if it could be shown that variations are not fortuitous in Darwin's sense of the word, but that natural selection is in some way provided with variation in those parts where change is needed.

Mivart has discussed this subject at considerable length. He points out that the modification of domesticated animals by the continued selection of slight variations, is a very slow process, and after quoting Darwin's statement that wild species probably change much more slowly than domesticated forms, he continues as follows: "Let us take for an example the proboscis monkey of Borneo. According to Mr. Darwin's own opinion, this form might have been sensibly changed in

the course of two or three centuries. According to this, to evolve it as a true and perfect species one thousand years would be a very moderate period. Let ten thousand years be taken to represent approximately the period of substantially constant conditions, during which no considerable change would be brought about. Now, if one thousand years may represent the period required for the evolution of this species and of the other species of the genus, ten times that period should, I think, be allowed for the differentiation of that genus, the African Circopithecus, and the other genera of the family Simiidæ, the differences between the genera being certainly more than tenfold greater than those between the species of the same genus.

". . . For the differentiation of the families Simiidæ and Cebidæ—so very much more distinct and different that any two genera of either family—a period ten times greater should, I believe, be allowed than that required for the evolution of the subordinate groups. A similarly increasing ratio should be granted for the successive developments of the difference between the Lemuroid and the higher forms of primates; for those between the original primates and other root-forms of placental mammals; for those between primary placental and implacental mammals; and perhaps, also, for the divergence of the most ancient stock of these and of the monotremes, for in all these cases modifications of structure appear to increase in complexity in at least that ratio. Finally, a vast period must be granted for the development of the lowest mammalian type from the primitive stock of the whole vertebrate sub-kingdom. Supposing this primitive stock to have arisen directly from a very lowly original animal indeed (such as a nematoid worm, an ascidian, or a jelly-fish), yet it is not

easy to believe that less than two thousand million years would be required for the totality of animal development by no other means than minute, fortuitous, occasional and intermitting variations in all considerable structures. If this be even an approximation to the truth, then there seem to be strong reasons for believing that geological time is not sufficient for such a process. . . . .

"Now, it will be a moderate computation to allow 25,000,000 years for the deposition of the strata down to and including the Upper Silurian. If, then, the evolutionary work done during this deposition only represents a hundredth part of the sum total, we shall require 2,500,000,000 (two thousand five hundred million) years for the complete development of the whole animal kingdom to its present state. Even one quarter of this, however, would far exceed the time which physics and astronomy seem able to allow for the completion of the process.

". . . Now all these difficulties are avoided if we admit that new forms of animal life of all degrees of complexity appear from time to time with comparative suddenness, being evolved according to laws in part depending on surrounding conditions, in part internal, similar to the way in which crystals (and perhaps, from recent researches, the lowest forms of life) build themselves up according to the internal laws of their component substance, and in harmony and correspondence with all environing influences and conditions."

Darwin himself seems to believe that in order to explain the harmonious co-ordination of all the inter-related parts of a complicated animal, we must believe that natural selection is greatly aided by other influences, such as the inherited effect of use and disease, the di-

rect action of external conditions, and especially the law of correlated variability.

Our theory of heredity furnishes exactly what we need to escape this difficulty, for we can understand that a change in any part of the body, disturbing, as it must, the harmonious adjustment of related parts, acts directly to produce variations in these parts in succeeding generations, by causing the transmission of gemmules. The time which is needed for the evolution of a complicated organ by natural selection is thus brought within reasonable limits, and one of the most serious and fundamental objections to Darwin's explanation of the origin of species is completely done away with.

He says: "We may borrow an illustration from Mr. Herbert Spencer, who remarks that when the Irish elk acquired its gigantic horns, weighing above one hundred pounds, numerous co-ordinated changes of structure would have been indispensable, namely, a thickened skull to carry the horns; strengthened cervical vertebræ with strengthened ligaments; enlarged dorsal vertebræ to support the neck, with powerful fore-legs and feet; all these parts being supplied with proper blood-vessels, muscles and nerves. How, then, could these admirably co-ordinated structures have been acquired? According to the doctrine which I maintain, the horns of the male elk were slowly gained through sexual selection, that is, by the best armed males conquering the worse armed, and leaving a greater number of descendants. But it is not at all necessary that the several parts of the body should have simultaneously varied. Each stag presents individual differences, and in the same district those which had slightly heavier horns, or stronger necks. or stronger bodies, or were the most courageous, would serve the greatest number of does, and consequently have the

greatest number of offspring. The offspring would inherit in a greater or less degree these same qualities; would occasionally intercross with each other, or with other individuals varying in some favorable manner; and of their offspring, those which were the best endowed in any respect would continue multiplying: and so onwards, always progressing, sometimes in one direction, and sometimes in another, towards the present excellent co-ordinated structure of the male elk.

"To make this clear, let us reflect on the probable steps, as shown in the twentieth chapter, by which our race and dray horses have arrived at their present state of excellence: if we could view the whole series of intermediate forms between one of these animals and an early unimproved progenitor, we should behold a vast number of animals not equally improved in each generation throughout their entire structure, but sometimes a little more in one point, and sometimes in another, yet on the whole gradually approaching in character to our present race or dray horses, which are so admirably fitted in the one case for fleetness, and in the other for draught.

"Although natural selection would thus tend to give to the male elk its present structure, yet it is probable that the inherited influence of use has played an equal or more important part. As the horns gradually increased in weight, the muscles of the neck, with the bones to which they are attached, would increase in size and strength; and these parts would react on the body and legs. Nor must we overlook the fact that certain parts of the skull and extremities would, judging from analogy, tend from the first to vary in a correlated manner. The increased weight of the horns would also act directly on the skull in the same manner as

when one bone is removed in the leg of the dog, the other bone, which has to carry the whole weight of the body, increases in thickness. But from the facts given with respect to horned and hornless cattle, it is probable that the horns and skull would immediately act on each other through the principle of correlation. Lastly, the growth and subsequent wear and tear of the augmented muscles and bones would require an increased supply of blood, and consequently an increased supply of food; and this again would require increased power of mastication, digestion, respiration and excretion."

It will be seen by a careful examination of this extract that Darwin is compelled, by cases of this kind, to believe that other influences have played a part equal to or more important than that of natural selection, and he is compelledto attribute the co-ordinated modification of related parts to the action of the law of correlated variability.

I have already called attention to the fact that this law of correlated variation is a necessary result of our view of the nature of heredity, for a change in one part must cause variation in co-ordinated parts; and gemmules thrown off by a certain organ of the body may cause co-ordinated variation in all the homologous parts of a descendant. I believe that it will be clear to every one, without further explanation, that the acceptance of our theory will greatly simplify our conception of the action of natural selection, and will enable us to understand the rapid evolution of co-ordinated structures, without being compelled to attribute them to other influences.

Darwin appears to have felt the need of something of the kind, for we find evidence that he has hunted long and faithfully, but in vain, for something to show that changed conditions produce, directly, the proper modi-

fications, and failing to find any such proof, he has accepted, as the only alternative, the view that variations are fortuitous. This is not the only alternative, for we see that there is a third view, namely, that changed conditions cause the variation, but do not determine its character.

In his exhaustive essay on *Variation*, Darwin has discussed the question whether the external conditions of life have such a direct and definite influence that the exposure of many individuals for many generations to any change in their physical conditions will result in the modification of all or nearly all of them in the same direction, thus producing a new sub-variety without the aid of selection.

He points out that many animals and plants which range widely and are exposed to great diversity of conditions remain nearly the same in character; that the two hundred plants which are distributed over every English county, and which must have been exposed for an immense period to considerable differences of climate and soil, are uniform throughout the whole area; and that certain birds, insects and plants which range over large portions of the world, nevertheless retain the same character.

He calls attention to the fact that fowls and pigeons have varied, and will no doubt go on varying, in directly opposite ways, though kept during many generations under nearly the same conditions; and he therefore concludes that the amount of modification which animals and plants have undergone under domestication does not correspond with the degree to which they have been exposed to changed circumstances. He lays especial stress, in this connection, upon the phenomena of bud-variation, and says: "It is well worth while to reflect

maturely on some striking case of bud-variation—for instance, that of the peach. This tree has been cultivated by the million in various parts of the world, has been treated differently, grown on its own roots and grafted on various stocks, planted as a standard against a wall, and under glass; yet each bud of each sub-variety keeps true to its kind. But occasionally, at long intervals of time, a tree in England, or under the widely different climate of Virginia, produces a single bud, and this yields a branch which ever after bears nectarines. . . . Now is it possible to conceive of conditions more exactly alike than these to which the buds on the same tree are exposed? Yet one bud alone, out of the many thousands borne by the same tree, has suddenly, without any apparent cause, produced a nectarine. But the case is even stronger than this, for the same flower-bud has yielded a fruit, one half or one quarter a nectarine, and the other half or three quarters a peach. Again, seven or eight varieties of the peach have yielded, by bud-variation, nectarines; the nectarines thus produced, no doubt differ a little from each other, but still they are nectarines. Of course there must be some cause, internal or external, to excite the peach-bud to change its nature; but I cannot imagine a class of facts better adapted to force on our minds the conviction that what we call the external conditions of life are quite insignificant, in relation to any particular variation, in comparison with the organization or constitution of the being which varies. We are thus driven to conclude that in most cases the conditions of life play a subordinate part in causing any particular modification; like that which a spark plays, when a mass of combustibles bursts into flame, the nature of the flame depending on the combustible matter and not on the spark. . . . Hence, although it must

be admitted that new conditions of life do sometimes definitely affect organic beings, it may be doubted whether well-marked races have often been produced by the direct action of changed conditions, without the aid of selection, either by man or nature" (*Variation*, 347–352).

While we acknowledge the great weight of this reasoning we must bear in mind that evidence to show that new forms of life are not produced, without the aid of selection, by direct modification, is not necessarily proof that the causes of variation have no relation to the purpose of the modification—that variations are, so far as their use goes, purely fortuitous.

Even if external changes do not give rise to useful modifications, unless they are aided by natural selection, it may still be true that they play an important and essential part.

It may be true that a change of conditions does not necessarily produce a change of structure, and yet true that when a change of structure does take place it is due to the changed conditions.

It may be true that an unfavorable change in the environment has no power to produce a compensating change of hereditary structure without the aid of natural selection, and yet true that this external change may be the cause of variation in the part affected.

If this latter supposition be a fact the work of natural selection will be almost infinitely simplified, for in place of an indefinite number of fortuitous variations, it will be furnished with variation of the part in which change is needed, and it is only an even chance whether a change in a part which is out of harmony with its environment be favorable or unfavorable.

According to our theory of heredity, when an organ-

ism, placed under new conditions, becomes modified to meet the change in its environment, the existence of the internal change is caused by the external change, while its precise character is determined by other factors, chiefly by the hereditary characteristics of the corresponding part, in both parents.

As long as the harmony which has been gradually established, by natural selection, between any particular cell and its conditions of life, remains undisturbed, this cell will continue to perform its function as a part of the body, and will have little tendency to give rise to gemmules. When through any change, either in the conditions of life external to the organism, or in other parts of the body, this cell comes to be placed in circumstances which are unfavorable to the performance of its function, it will exert the tendency to throw off gemmules; for each cell being, in a morphological sense, an independent organism, possesses this power, by inheritance, although natural selection has gradually acted, during the past history of the evolution of life, to prevent the useless manifestation of the tendency, as long as surrounding conditions are favorable and no change is needed.

These gemmules, when transmitted to the egg, by impregnation, will, by sexual union with the corresponding parts of the egg, cause variation in the homologous cells of the offspring, and will thus produce a congenital hereditary change at the very time when, and in the very part where, such change is needed.

Instead of being purely fortuitous on the one hand, or due on the other hand to the direct modifying influence of external conditions, congenital variations are due to the manifestation of a general law, which has gradually become established, during the evolution of

life, for this very purpose. I believe that the gradual establishment of this law of heredity is due to the action of natural selection; to the divergent specialization of the two sexual elements; and to a physiological division of labor, each step in the production of which has been advantageous, and has therefore been perpetuated like any other useful variation.

According to this view, we must recognize in the law of natural selection, not simply a great means of modification, but the agency to which organic evolution is almost exclusively due; but we must also believe that, in the higher multicellular organisms it acts indirectly, and is subordinate to another law, the law of heredity, which itself owes existence to the law of natural selection.

Objection to the View that the Variation of any Part is Caused by the Transmission of Gemmules, which owe their Existence to the Action of Unfavorable Conditions upon the Corresponding Part of the Parent.

Mr. H. W. Conn has called my attention to the fact that in many cases it is difficult to see any connection between the function of a new variation and a failure to perform that function in the parent. He instances the mimetic colors of insects, and the long neck of the giraffe, and says that it is difficult to see how the action of unfavorable conditions upon the parents could have given rise to these variations. He says that if an insect were dangerously conspicuous its unfavorable conditions of life would not affect the cells to which its color is due, in any especial way, but would lead to the destruction of the entire animal.

So, too, if a series of dry seasons should place the giraffe under conditions of hardship, the individuals

with the shortest necks would suffer most, from inability to reach their food, but he says that this would not affect the cells of their necks especially, but would result in general disadvantage to the whole body.

The validity of this objection cannot be denied, and I do not think it would be difficult to find many instances which are much more striking than the two which have been referred to.

It is very difficult to understand how our explanation of the origin of variation can apply to instances of modification in animals which, like worker bees, do not produce descendants.

It is proper to point out, however, that these cases are no more difficult to explain after our theory of heredity is accepted than without it. Its acceptance does, in many cases, greatly simplify our conception of natural selection, and the fact that it still leaves difficulties unexplained, is no reason for rejecting it, provided it does not add to these difficulties.

In the case of the giraffe it is not difficult to understand that if circumstances should compel this animal to stretch frequently after foliage almost beyond its reach, this might cause hardship in the cells of the neck, and thus result in the production of gemmules, and in consequent variation of this part of the body.

As sterile insects are simply sexual insects which have not become perfectly developed, we must believe that all their characteristics are shared by the sexual insects, and there is therefore no great difficulty in understanding how the action of unfavorable conditions upon the sexual form might cause variation in the sterile form.

The various cells of the body stand in such intimate relations to each other, and are mutually dependent upon each other in so many ways, that it is quite impos-

sible to trace out in its completeness the effect of an external influence. A change outside the body may have an obvious and direct effect upon the cells of a certain part, and these cells may influence other cells and so on indefinitely. Any of the cells which are thus affected may give rise to gemmules, and may thus result in a favorable variation which will be seized upon and perpetuated by natural selection. A new variation may therefore follow from an external change which has no direct influence upon the part in which the variation occurs. This would be an apparent but not a real objection to our view that the cause of a variation is to be sought in the unfavorable action of changed conditions upon the part in which the variation occurs, but our inability to trace the connection between a variation and the external change to which it is due, is no reason for doubting the reality of the connection.

Saltatory Evolution.

The origin of species by the natural selection of minute fortuitous variations, demands time which is so long that it is practically infinite, and many naturalists have accordingly held that the successive changes may possibly not be so minute as Darwin believes. Thus Huxley says: "We greatly suspect that Nature does make considerable jumps in the way of variation now and then, and that these saltations give rise to some of the gaps which appear to exist in the series of known forms."

Galton compares the evolution of an organism to the rolling of a rough stone, which has, in consequence of its roughness, a vast number of natural facets on any one of which it might rest in stable equilibrium. When pushed, this stone would yield a little; but it would fall back again on the withdrawal of the pressure, unless this

was great enough to overpass the limit of the facet on which it has been resting.

In this case it would tumble over into a new position of stability, which it will retain until the pressure again becomes great enough to dislodge it and roll it another step onwards. He says, "The various positions of stable equilibrium may be looked upon as so many typical attitudes of the stone, the type being more durable as the limits of its stability are wider. We also see clearly that there is no violation of the law of continuity in the movements of the stone, though it can only repose in certain widely separated positions."

Mivart, who has discussed this subject at some length, has given many reasons for believing, in opposition to Darwin, that such sudden jumps do occur, and that evolution is not always by minute changes.

It is clear to every one that any theory of the cause of variation, which recognized the possibility of sudden and extensive modification, would very greatly diminish the time which is demanded for the origin of species by natural selection, and would thus greatly simplify our conception of the working of this law.

We have just seen that as our theory of heredity explains how a variation in one part causes related parts to vary, it removes one great objection to the theory of natural selection, and I wish now to call attention to the fact that, since a change in any part will disturb the harmony of related parts, thus causing their cells to throw off gemmules, a slight change in one generation may become, in following generations, a very considerable modification. There is therefore no reason why natural selection should not often be presented with great and extended variations—the saltations which Mivart believes in—and the evolution of organisms may

therefore be a much more rapid process than Darwin believes.

We will now examine the evidence to show that sudden changes of this kind do sometimes occur. This evidence is of necessity drawn almost entirely from our domesticated animals and plants. A great gap between fossil forms might be attributed to the imperfection of the record, and if a wild form were to come into existence suddenly it would simply be recorded as a very rare species, and there would be no way to tell whether it is the first or the last of its race. If a considerable modification of a well-known wild species should appear suddenly in a region which is well known and thoroughly explored, we might have sufficient evidence to be certain that it is due to recent variation: and there are a few instances of this kind, the spike-horned buck of the Adirondacks being the most conspicuous one with which I am acquainted. In Dec., 1869, a writer in the *American Naturalist* says that he has hunted in the Adirondacks where the Cervus Virginianus abounds for the last twenty-one years. About fourteen years ago he first heard of spike-horn bucks. These became from year to year more common; about five years ago he shot one, and subsequently another, and now they are frequently killed. He says that the spike-horn differs greatly from the common antler of C. Virginianus. It consists of a single spike, more slender than the antler, and scarcely half as long, projecting forward from the brow, and terminating in a very sharp point. He believes that it gives a considerable advantage to its possessor over the common buck, as it is a more effective weapon than the common antler, at the same time that it enables him to run more swiftly than the common buck through thick woods and underbrush.

This certainly seems to be an instance of the sudden appearance, in a wild species, of a very considerable modification, and although it is true that few similiar instances have been recorded, the study of variation in domesticated animals leads us to believe that many similar cases must occur in wild forms, although our means of observation do not allow us to prove that this is the case.

In 1791 a ram-lamb was born in Massachusetts, having short crooked legs and a long back, like a turnspit dog. From this one lamb the well-known ancon breed of sheep was raised (Darwin, *Variation*, I. p. 126). Darwin says that in 1828 a single ram-lamb was born on the Mauchamp farm with long, smooth, straight silky wool. The ram was of small size, with a large head, long neck, narrow chest, and long flanks. This one ram is the founder of the Mauchamp-merino breed of sheep, and has transmitted all his desirable peculiarities to a whole race of descendants, although certain undesirable peculiarities have been eliminated by judicious selection.

Darwin says (*Variation*, I. p. 350): "There is one strange fact with respect to the peacock, namely, the occasional appearance in England of the 'japanned' or 'black-shouldered kind.' This form has lately been named on the high authority of Mr. Sclater as a distinct species, *Pavo nigripennis*, which he believes will hereafter be found wild in some country, but not in India, where it is certainly unknown. These japanned birds differ considerably from the common peacock in the color of their secondary wing-feathers, scapulars, wing coverts and thighs; the females are much paler, and the young, as I hear from Mr. Bartlett, likewise differ. They can be propagated perfectly true. Although they do not resemble the hybrids which have been raised between

P. cristatus and *muticus*, nevertheless they are in some respects intermediate in character between these two species; and this fact favors, as Mr. Sclater believes, the view that they form a distinct and natural species.

On the other hand, Sir H. Heron states that this breed suddenly appeared within his memory in Lord Brownlow's large stock of pied, white, and common peacocks. The same thing occurred in Sir J. Trevelyan's flock composed of common and pied peacocks. It is remarkable that in these two latter instances the black-shouldered kind increased to the extinction of the previously existing breed. I have also received, through Mr. Sclater, a statement from Mr. Hudson Gurney that he reared, many years ago, a pair of black-shouldered peacocks from the common kind, and another orinthologist, Prof. A. Newton, states that, five or six years ago, a female bird, in all respects similar to the female of the black-shouldered kind, was produced from a stock of common peacocks in his possession, which, during more than twenty years, had not been crossed with birds of any other strain. Here we have five distinct cases of japanned birds suddenly appearing in flocks of the common kind kept in England. Better evidence of the first appearance of a new variety could hardly be desired. If we reject this evidence, and believe that the japannned peacock is a distinct species, we must suppose in all these cases that the common breed had at some former period been crossed with the supposed *P. nigripennis*, but had lost every trace of the cross, yet that the birds occasionally produced offspring which suddenly and completely reacquired, through reversion, the characters of *P. nigripennis*. I have heard of no other such case in the animal or vegetable kingdom. . . . So remarkable a form as *P. nigripennis*, when first imported, would have

realized a large price; it is therefore improbable that it should have been silently introduced, and its history subsequently lost. On the whole the evidence seems to me, as it did to Sir H. Heron, to preponderate strongly in favor of the black-shouldered breed being a variation, induced either by the climate of England or by some unknown cause, such as reversion to a premordial and extinct condition of the species. On the view that the black-shouldered peacock is a variety, the case is the most remarkable ever recorded of the abrupt appearance of a new form which so closely resembles a true species that it has deceived one of the most experienced of living ornithologists."

Mivart quotes from Naudin, Godron, and others, several very similar cases in plants. From the seeds of a poppy, which suddenly took on a remarkable variation in its fruit, a crown of secondary capsules being added to the normal central capsule, a field of poppies was grown. These resembled the form from which the seed was taken, and gave seed which again reproduced the variation. In 1861 Godron "observed among a sowing of *Datura tatula*, the fruits of which are very spinous, a single individual of which the capsule was perfectly smooth. The seeds taken from this plant all furnished plants having the character of this individual." These seeds were cultivated up to the fifth and sixth generations, and the latest descendants did not exhibit the least tendency to revert to the spinous form.

These cases show us that very considerable variations may suddenly appear in cultivated plants and domesticated animals, and that these sudden modifications may be strongly inherited, and may thus give rise to new races by sudden jumps.

The analogy of domesticated forms would lead us to

believe that the same thing sometimes occurs in nature, and that Darwin has over-estimated the minuteness of the changes in wild organisms, and has thus failed to see that natural selection may give rise to new and well-marked races in a few generations.

Our theory of heredity would lead us to expect much of this sudden modification, and it gives us a simple explanation of its origin, and thus gives to the law of natural selection a much simpler and therefore a much more probable form than that in which it presented itself to the mind of its discoverer.

Parallel Variation.

According to the view that variations are purely fortuitous, the chances are almost inconceivably great against the independent modification of several forms along parallel lines, by the action of natural selection, yet Darwin gives many instances in which this has actually occurred.

He says that by the term "analogous or parallel variation" he wishes to express that similar characters occasionally make their appearance in the several varieties or races descended from the same species, and more rarely in the offspring of widely distinct species. For instance the nectarine is the offspring of the peach; and the varieties of both these trees offer a remarkable parallelism in the fruit being white, red or yellow-fleshed, clingstone or freestone, in the flowers being large or small, in the leaves being serrated or crenated, furnished with globose or reniform glands, or quite destitute of glands. In this case we know that the two forms have independently varied in parallel lines, and that each variety of the nectarine has not derived its character from a corresponding variety of the peach. The several varieties of

the apricot, which belongs to a closely allied genus, differ from each other in nearly the same parallel manner. Darwin gives many similar instances, and we must acknowledge that in these cases we have homologies which are not due to inheritance from a common ancestor, but to secondary modification.

It is true that, in all the cases which Darwin gives, the parallelism exists between forms which are very much alike, and which have quite recently diverged from a common ancestor, but there is reason to believe that this is not always the case. Morphologists assume that homology or morphological resemblance is, in itself, evidence of community of descent, and when two widely separated organisms present features which show fundamental similarity of plan, they take it for granted that they owe their resemblances to inheritance from a common ancestor, which exhibited all the characteristics which they share in common.

This is no doubt true as a general rule, and even if it were not true it would usually be extremely difficult to prove its falsity; but there are a few cases where great groups of animals are related to each other in such a peculiar way that the view that all their homologies are due to descent is untenable.

The Medusæ present such a case. These animals resemble each other in many particulars. They have a muscular contractile gelatinous umbrella by the pulsations of which they swim through the water. The digestive organs are suspended from the concave centre of the umbrella, and they give rise to diverticula which penetrate its gelatinous substance. Their reproductive organs are developed upon the digestive tract or upon its diverticula, while their organs of sense are placed around the margin of the umbrella. They usually pass

through a fixed polyp-like larval stage before maturity is reached, and this polyp larva is destitute of a swimming umbrella, and of organs of special sense. It has an elongated cylindrical body, by one end of which it is attached, while the mouth is placed at the opposite end and is surrounded by a crown of tentacles.

The group is divided into two grand divisions, the medusæ with a veil or diaphragm across the opening of the umbrella, and the medusæ without a veil. The two groups resemble each other in all essential particulars, and no naturalist has doubted that they are truly homologous with each other, but they present certain constant differences, such as the presence of a veil and the absence of gastric filaments in the one group, and the absence of a veil and the presence of gastric filaments in the second group. The larva of a veiled medusæ is a hydroid-polyp, which has a simple digestive cavity, and the power of multiplication by lateral budding, while the polyp-larvæ in the veilless medusæ is known as a scyphostoma. It has gastric filaments in its digestive cavity, and it multiplies by terminal budding or fission. In other respects, the two kinds of larvæ show a close homology with each other, but the points of resemblance are not the same as those which unite the two groups of mature medusæ.

Haeckel has devoted many years to the study of the medusæ, and his opinion is entitled to very great weight, and he believes that the resemblances between the larvæ are due to community of descent, but that the resemblances between the adults are not. He believes that the remote ancestor of all the medusæ was a polyp which united in itself the features which now distinguish the hydra-larvæ of the veiled medusæ from the scyphostoma larvæ of the veilless forms, and that these

two larval forms have diverged in two directions from this ancestor, from which they inherit all that they have in common.

Haeckel believes that after this separation took place, the veiled medusæ were developed from hydroid polyps, while the veilless medusæ were developed from scyphostoma polyps. The many points of resemblance between the two forms of medusæ are, therefore, not due to common inheritance, but have been secondarily acquired. They are due to the fact that the two groups of medusæ have been evolved along parallel but distinct lines.

Haeckel's familiarity with the medusæ entitles him to speak with great authority; but still he may possibly be wrong, and the origin of the two groups may not have been as he supposes.

There are four possible hypotheses as to the origin of the medusæ, in favor of each of which something may be said. We may hold with Haeckel that the two larval polyps are the divergent descendants of a common ancestral polyp, which had no medusa stage, and that each has subsequently developed medusæ, or we may believe that the common ancestor was a medusa without a polyp larva, and that the hydra larva and the scyphostoma larva have been independently acquired, or we may believe that the ancestral form had both a larval polyp-like stage, and an adult medusa stage, or finally we may assume what seems to us the most probable view, that the ancestral form was neither a true swimming medusa nor a true sedentary polyp, but something half-way between, like the actinula of Tubularia or the embryo of Turritopsis. I do not see any fifth alternative, and one of these four suppositions must correspond with the actual evolution of the group. Now

whichever one we accept, we are compelled to believe that there has been parallel evolution, and that certain homologies between the various forms are not due to inheritance, but to independent modification.

Haeckel's view compels us to believe that the resemblances between the two groups of medusæ have been independently acquired. If we accept the second alternative, and derive the two forms from an ancestral medusæ, the resemblances between the larvæ must be due to parallel variation. Suppose, then, that we accept the third or the fourth view, and derive both groups from an ancestral form which had a polyp-like larval stage, and a medusa-like adult stage, or else from an ancestral form which united in itself certain of the larval and certain of the adult characters.

Among the veiled medusæ there are some which, like Liriope, do not pass through a hydra stage, but lay eggs, which develop directly into medusæ; and there are also forms which, like the fresh water hydra, have no medusæ stage. Among the veilless forms there are also some which have no medusa stage, but which, like Lucernaria and the Tesseridæ, remain permanently as scyphostoma-polyps, and it is probable that in others, as the Charybdeadæ, the eggs hatch into medusæ, as they do in Liriope, without the intervention of a larval polyp stage.

It is therefore impossible to frame any hypothesis as to the origin of the medusæ, which will do away with the necessity for the belief that parallel modification, along independent lines, has occurred in the different subdivisions of the group.

If we accept Darwin's view of the origin of variation, parallel modification is not absolutely impossible, although the chances against it are very great indeed.

The cases where it can be proved to have occurred are not very numerous, it is true, but there are enough of them to present a serious difficulty. On our view that an external change which acts upon a certain part of the body may cause variation in that particular part, the chances against the parallel modification of allied organisms are very greatly diminished, so much so that the occasional occurrence of such modifications might be expected. If such cases were the rule they would be equally fatal to the theory of natural selection, whether our theory of heredity were accepted or not; but the cases are very far from frequent.

General and Special Homology: and the Significance of Serial Homology, Symmetry and Polymorphism.

We have, so far, been occupied in studying the evidence for the law of heredity which is afforded by the slight and recently acquired differences between the sexes of the same species, between the young and the adult, between domesticated and wild races, between the hybrid offspring of allied species, between reciprocal hybrids, etc.

The bearing of this law upon the more profound problems of morphology has hardly been referred to, for the field which we have examined, although we have passed over it very rapidly, has furnished material for a treatise of considerable length. The discussion of the general problems of morphology would require another volume of even greater length, for I believe, and hope to show in another place, that the acceptance of my view will lead to considerable change in our manner of handling these problems; and will so shift our view as to remodel some of the fundamental principles of the science.

I believe that it will throw light upon many obscure and perplexing questions, such as the significance of

symmetry and general homology, the origin of polymorphism, the definition of an individual or person, etc.; but the end of a book is not the place to enter upon a a new field, and I am forced to reserve this subject for future discussion, although I will now indicate very briefly the nature of this explanation.

The basis of modern morphology is the doctrine that homology indicates genetic relationship.

Homology is fundamental similarity of plan, as distinguished from difference or similarity in physiological function. For example a man's arm and hand are fitted for grasping, and a bird's wing for flight, and their different uses render them unlike each other in a superficial view, although there is below and behind this obvious difference a more deep-seated resemblance. The feathers which cover the bird's wing have the same histological structure and the same origin as the hairs upon the human arm; the skin which covers the limb has the same character in both cases; the wing, like the arm, has a supporting skeleton, which consists of a shoulder and upper arm, a forearm, a wrist, and a hand; the muscles have the same structure and the same general arrangement, and the way in which they are supplied with nerves and blood-vessels is the same.

This fundamental identity of structure which is obscured, but not destroyed by the difference of use, is homology. In a superficial view the wing of a bird resembles the wing of a dragon-fly more closely than it resembles a man's arm, but careful examination shows that the insect's wing is not a limb at all, but a peculiar outgrowth from the body. The resemblance between a bird's wing and an insect's wing is not an homology, and it has no morphological significance: it does not indicate that there is any close relationship between a bird and an insect.

It is sometimes difficult to determine whether a resemblance is an homology or not, and in simple cases we decide by asking whether it can be due to similarity of use. We know that a bird's wing is more closely related to a man's arm than it is to an insect's wing, because the resemblance between the two wings is no more than we should expect in organs adapted to the same purpose; but there is nothing in the use of the arm and wing to explain what they have in common.

In cases too complicated to be settled in this simple way we appeal to embryology, and ask whether the resemblance becomes more marked or less marked when we study it in its younger stages. The arm and the wing are more alike in the embryo than they are in the adults, and the features which they share in common make their appearance earlier than their distinctive characteristics.

An homology then is a resemblance which is not due to similarity of use, and which is more conspicuous in the embryo than in the adult.

This is the doctrine of homology considered from its structural side; historically considered, an homology is a resemblance due to community of descent, as distinguished from one due to recent modification. The modern morphologist believes that the resemblances between a bird's wing and a man's arm are due to inheritance from a remote ancestor in which the limb had all the characteristics which are common to the wing and arm; that during the evolution of birds and mammals along two divergent lines from this ancestral form, the distinctive features which fit the wing for flight and the hand for grasping have been gradually acquired.

The doctrine that homology is an indication of ancestral relationship, and that the past history of organisms

can be traced by studying their anatomy and embryology, is the basis of the modern science of morphology.

Now there are two kinds of homology, special homology and general homology. Homologies between corresponding parts of different animals are known as special homologies, and those between different parts of the same animal as general homologies. As examples of general homology we may instance the serial homology of a cray-fish, the bilateral symmetry of mammals, and the radial symmetry of a star-fish.

So far as structure goes the homology between a man's arm and a man's leg is precisely like the homology between his arm and a bird's wing. It is a resemblance which is not due to similarity of use, but to fundamental resemblance, and it is more marked in the embryo than it is in the adult, and we seem, at first sight, to be justified in concluding that, if special homologies indicate genetic descent, general homologies must also; and that if general homologies cannot be explained in this way, the explanation of special homologies cannot be accepted.

Mivart has pointed out that it is impossible to explain general homologies by attributing them to inheritance from a common ancestor, and he therefore concludes that special homologies do not prove genetic evolution. On the other hand many authors have held that since special homologies indicate descent, general homologies must have the same meaning, and this belief has led to such speculations as the attempt to trace the vertebrates back to an annelid with a number of equivalent segments, to trace the echinoderms back to a community of worms, and to trace the polymorphic siphonophores back to unspecialized communities of hydroids.

I hope to show in another place that the acceptance

of my view of the nature of heredity enables us to avoid both of these results, since it shows that special homologies may be due to heredity of one sort, and general homologies to heredity of another sort. Since corresponding cells in the homologous parts of the body of any individual are derived from closely related parts of the egg, they may be affected by similar gemmules and may thus give rise to what Darwin calls analogous variations. This form of inheritance I propose to call ontogenetic heredity, to distinguish it from ordinary inheritance from an ancestor. I shall point out, in another place, that while special homologies are due to ordinary or phylogenetic heredity, that is, to descent from a common ancestor, general homologies are, in many cases, due to ontogenetic heredity; that special homologies are old, and that they indicate genetic relationship, and thus enable us to trace the origin and history of animals, while general homologies are, in many cases, new, and recently acquired by secondary modification, and they do not indicate ancestry.

CHAPTER XII.

RECAPITULATION AND CONCLUSION.

THE obscurity and complexity of the phenomena of heredity afford no ground for the belief that the subject is outside the legitimate province of scientific inquiry. The existence, in a simple and unspecialized egg, of the potentiality of a highly organized and delicately adjusted animal, with special functions, instincts and powers of adaptation, with the capacity for establishing and perpetuating harmonious relations to the changing conditions of the world around it, is certainly one of the most profound problems of the material universe.

The fertilized egg is one of the greatest wonders within our knowledge, but this is no reason for refraining from studying it.

If we believe that living things have become what they now are by a process of gradual evolution, and that they owe their characteristics to the influences to which they have been exposed in the past, we must believe that the properties of the egg are capable of explanation, as far as these determining causes are open to study.

If we accept the generalizations of modern science, and hold that an unicellular ovum is homologous with and is descended from a remote ancestral unicellular organism, and that its properties have been gradually acquired by the natural selection of favorable variations, we must believe that the origin of its properties is as much within our reach as the origin of species.

The most prominent characteristic of heredity is that

it may be brought about not only by the various forms of asexual reproduction, but also by the sexual union of two reproductive elements, each of which is homologous with the other cells of the body.

In the lower animals and plants the cells which thus unite with each other, or conjugate, are similar in form, and probably in function also; but in all the higher organisms the male cell is very different from the ovum in form, size, and structure, as well as its mode of origin.

The present structure of each organism is the resultant of two factors, which we may call adherence to type and adaptation to new conditions, or if the use of terms without teleological implications is desired, we may speak of them as heredity and variation, or we may follow Haeckel and call them memory of past experiences, and perception of new relations. The precise terms to be used is a matter of little consequence. The essential thing is the recognition of the fact that each organism is the resultant of two factors, and that evolution is two-sided. An animal is what it is because it has the power to hold on to the experiences and adaptations which fitted its parents for their place in nature, and the parents acquired those peculiarities in virtue of their powers to gradually adjust their structure and habits to their environment.

This is the morphological side of evolution. Looking at it from its dynamical or functional side, we notice that each step in the process of advancement has been reached by divergent specialization and by physiological division of labor. Animals diverge from each other by acquiring the power to occupy different fields, to procure and use different kinds of food, to exist in different media, etc., and the organs and tissues and cells of a highly specialized animal or plant are adapted to perform

definite, restricted functions exactly and efficiently, while each part of a low organism fills many offices, but fills them all imperfectly.

We find in all except the lowest organisms that heredity is brought about by two dissimilar reproductive elements, and we find that each organism is the resultant of two factors—heredity and variation.

It is natural to inquire whether there may not be some connection between these two relations; whether the natural selection of favorable variations has not acted upon the reproductive elements as it has upon the mature organisms; whether it has not brought about a physiological division of labor between these elements; whether their originally similar functions have not gradually become specialized until one has become the conservative medium, and the other the agent of progress in heredity.

According to the view advocated in this book, such has actually been the history of the evolution of sex, and natural selection has evolved, in all the higher organisms, a secondary law of heredity, which enables it to do its work rapidly and effectively, with little waste.

In the metazoa and in the higher plants, natural selection is not a crude, rough "hit or miss" method of evolution, for the law of heredity, itself a result of the law of natural selection, is that the ovum is the vehicle of heredity, while gemmules or cell-germs from cells in all parts of the body, are transmitted to the ovum by the male cell, thus causing variation when and where it is needed.

This view is opposed to the conclusion of many high authorities that there is no difference in the functions of the sexual elements, but examination shows that the reasons which they have given for this conclusion admit of another simple explanation.

Darwin's reason for his statement that each sexual element has the power to transmit every single characteristic of the parent form, and that it is an error to suppose that the male transmits certain characters and the female other characters, is that when hybrids are paired and bred *inter se*, the characters of either grandparent often reappear in the progeny.

A little thought will show that it is impossible to prove any such conclusion in this way. If two animals which differ from each other in every respect could be made to cross, the result would furnish conclusive evidence as to the correctness or incorrectness of Darwin's statement, but in any possible cross the parents are essentially alike, and they differ only in minor features of recent acquisition. The possibility of parthenogenesis proves that the ovum does transmit the entire organization, but it is impossible to show, from the phenomena of crossing, that the male element has the same power.

The reason given by Huxley for his opinion that an animal inherits every characteristic of each parent, is that the ovum and the male cell are homologous with each other, and that all the cells of the body are descended, by a process of division, from the compound germ which is formed by their union.

Homology, or similarity of origin, is no ground for assuming similarity of function, and the fact that the male cell and the egg are homologous with each other is no reason whatever for a belief that their parts in heredity are alike.

The fact that either sex may, under certain circumstances, acquire the secondary sexual characters of the other, seems at first sight to show that the whole organization of the male exists in a potential and latent state in the body of every female, and that the whole organi-

zation of the female is latent in every male; that each individual is a complete double person. If we accept this conclusion it is only logical to conclude that the power to revert or acquire the characteristics of remote ancestors proves the existence, in a latent state, in each individual, of the complete organization of each of a long series of ancestors of both sexes.

This subtle metaphysical conception is so foreign to the methods and tendencies of modern thought, that when we compare it with Hunter's simple and definite statement that the natural history characteristics of any species of animal are to be found in those properties that are common to both sexes, there does not seem to be any room for choice. The view that each individual inherits all the characteristics of the species, and that the distinctive characteristics of the male are arrested in certain ones, while the distinctive features of the female remain latent in others, furnishes a simple and adequate explanation of the facts, and removes all necessity for the subtle, complex and unthinkable, compound personality hypothesis.

In this connection the interesting and practical question, what determines the sex of the embryo, can hardly fail to suggest itself to the reader. I have refrained from a discussion of this important point in the body of this work, as it has no direct bearing upon our argument and I have no solution to offer. As I have so far omitted all reference to the subject, I will take occasion now to call attention, in this connection, to the facts detailed on pp. 55–69. The reader will see that all female bees are born from fertilized eggs, and all male bees from unfertilized eggs; while the unfertilized eggs of daphnia give rise to females only, and in many of the gall wasps both males and females are born from parthonogenetic eggs. There

is no necessary or constant connection between the fertilization of the egg and the sex of the embryo, and the conclusion which I have reached from the study of these cases and of our scanty information upon the subject from other sources, is that sex is not determined by any constant law; that in certain animals and plants the sex of the embryo is determined by certain conditions, while in other groups it is determined by quite different conditions.

However this may be, it is obvious that since perfect males and perfect females may arise from eggs which are fertilized, and also from eggs which are not fertilized, the necessity for fertilization does not come from the necessity for transmitting to the offspring the organization of each parent.

A review of the opinions and reasoning of various authors shows that there is no good ground for believing that the two reproductive elements play similar parts in heredity and transmit every characteristic of each parent. It is impossible to prove it by the phenomena of crossing, since the only animals which can be made to cross are essentially alike, and differ only in minor points. The homology between the ovum and the male cell is no reason for supposing that their functions are similar. There is no reason for assuming that each sex transmits its entire organization to the offspring, since the latent transmission of secondary sexual characters can be more simply explained by assuming that each embryo inherits, but does not necessarily develop, all the characteristics of its species.

Reversion and alternation of generations admit of a similar explanation, and we may conclude that there is and can be no proof that each sexual element transmits all the characteristics of the parent. There is therefore

no *a priori* absurdity in the hypothesis that the ovum and the male cell fill different offices. While there is no reason for believing that the functions of these elements are alike, there are many reasons for believing that this is not the case; for example, the almost universal occurrence of differences in form, size, and structure; the possibility of parthenogenesis; the differences between reciprocal hybrids; the fact that the offspring of a male hybrid and a female of a pure species is much more variable than the offspring of a female hybrid by the male of a pure species; and the fact that a part which is more developed or is of more functional importance in the male parent than it is in the female parent, is much more apt to vary in the offspring than a part which is more developed or more important in the mother than it is in the father.

In the absence of all evidence to the contrary I think we may safely conclude from this positive evidence that a division of physiological labor has arisen during the evolution of life, and that the functions of the reproductive elements have became specialized in divergent directions.

The only way to discover the exact nature of this specialization is to study the influence of each element separately, and the comparison of sexual with asexual reproduction is the best available method of doing this, since asexual reproduction is essentially reproduction without a male element, while sexual reproduction is reproduction with a male element.

Organisms produced from fertilized ova differ from those produced asexually only in their greater tendency to vary, and the hypothesis that the male element has become specialized for the transmission of a tendency to vary naturally suggests itself. Variation is not dependent upon fertilization, for plants produced from buds

vary as well as those born from fertilized seeds, although bud variations are extremely rare as compared with seedling variations.

In any attempt to frame an hypothesis of heredity we must therefore recognize all the following facts: that the two reproductive elements are homologous, and that their functions were originally alike; that the possibility of parthenogenesis, together with many other well ascertained facts, shows that their functions are not alike, in the higher organisms, at present; that their present functions are due to divergent specialization or physiological division of labor; that variation is possible without sexual union, but that the introduction of a male element in reproduction greatly increases the frequency of its occurrence.

Among the unicellular organisms variability is provided for by conjugation, or the fusion of two entire individuals so that the new generation is derived from a compound germ which contains particles to represent all the parts of the body of each parent. In the metazoa and the many celled plants the reproductive bodies are localized and they are single cells, and there must therefore be some mechanism or organization in virtue of which they represent cells from all parts of the body, and thus provide for further variation.

These various considerations have led us to believe that each cell of the organism inherits from its unicellular ancestors the power to throw off cell germs or gemmules; that these germs penetrate to all parts of the body, and that those which thus reach the developing reproductive elements insure variation, in the next generation, in the cells which they represent; that originally the two sexual elements were alike in function; that each inherited from the fertilized ovum of the pre-

ceding generation the power to give rise to a new organism with all the established hereditary characteristics of the race; and that each element also had, by virtue of its contained gemmules, the power to transmit variability.

The existence, in each element, of the power to transmit the hereditary characteristics of the species is obviously superfluous, since the object of sexual union, the transmission of a tendency to vary, would be equally well secured if only one element had the power to transmit the common characteristics of both parents. I therefore believe that, as organisms gradually increased in size, as the number of cells in their bodies grew greater, and as the differentiation and specialization of these cells became more and more marked, one element, the male cell, became adapted for storing up gemmules, and, at the same time, gradually lost its unnecessary and useless power to transmit hereditary characteristics. This process was gradual, and even in the highest animals the power of the male cell to transmit hereditary characters does not seem to be completely lost, although few traces of it remain.

I also suppose that natural selection has acted upon the various cells of the body to restrain them from throwing off unnecessary gemmules, and that this power is exercised only when a change in the surrounding world renders variation necessary.

After framing this hypothesis the next step is to test it by applying it to the various observed phenomena of heredity in order to see how far it explains and interprets them. I have attempted to do this in chapters VI. to X. of this book, and I think we are justified in concluding, as the result of this review, that, while there are many facts which the hypothesis does not explain, they are not of such a character as to directly contradict it, while it

does group and illuminate many classes of facts which are quite inexplicable without it.

The evidence from hybrids seems to be strongly in its favor, and it presents many features which are perfectly simple and natural, according to our view of heredity, although no other explanation of them has ever been offered.

Hybrids and mongrels are highly variable, as we should expect from the fact that many of the cells of their bodies must be placed under unnatural conditions, and must therefore have a tendency to throw off gemmules. Darwin's pangenesis hypothesis accounts for the variability of hybrids, but it does not account for the very remarkable fact that hybrids from forms which have long been cultivated or domesticated are more variable than those from wild species or varieties, or for the fact that the children of hybrids are more variable than the hybrids themselves.

Our view not only explains the variability of hybrids, but it also accounts for the excessive variability of hybrids from domesticated forms, and of the children of hybrids, for domesticated animals and plants live under unnatural conditions, and they are therefore more prolific of gemmules than wild species, and as the body of a male hybrid is a new thing the cells will be much more likely than those of the pure parent to throw off gemmules.

The fact that variation is due to the male influence, and that the action upon the male parent of unnatural or changed conditions results in the variability of the child, is well shown by crossing the hybrid with the pure species, for when the male hybrid is crossed with a pure female the children are much more variable than those born from a hybrid mother by a pure father.

The remarkable history of reciprocal crosses is, on the whole, exactly what we should expect, and although there are many difficulties, they are no greater than the complexity of the subject would lead us to anticipate.

The study of variation brings out a number of secondary laws, all of which might have been derived from our view of the nature of heredity.

The law that sexual offspring are more variable than those produced asexually has just been discussed, and it is clearly in perfect accordance with our view.

Another most interesting and remarkable law—that changed conditions do not act directly, but that they cause subsequent generations to vary—receives a simple explanation as soon as we recognize that variation is due to the transmission of gemmules, not to the direct modifying influence of external conditions.

We can also understand why variation should itself be hereditary, why specific characters should be more variable than generic characters, why species of large genera should vary more than species of small genera, why a part developed to an unusual degree or in an unusual way should also be extremely variable, and why secondary sexual characters should show a marked tendency to vary.

The study of secondary sexual characters aids us, like the study of hybrids and of variation, to analyze or disentangle the influences of the two sexes in heredity. These characters, therefore, possess especial interest in connection with our subject. They are found, upon examination, to present many striking peculiarities which might have been directly deduced from our view of the nature of heredity.

As gemmules which are formed in the male body are much more likely to be transmitted to descendants, and

thus to give rise to variation, than gemmules which are formed in the female body, we should expect to find, in a variation which first appears in a male, much more tendency to become hereditary than in a variation which first appears in a female. For the same reason we should expect to find an organ which is confined to males much more likely than one confined to females to give rise to hereditary modifications.

For a similar reason we should expect the males of unisexual animals to vary more than the females.

We can form some conception of the amount of modification which an animal has recently undergone by comparing the adults with the young, and by comparing allied species with each other.

When we make comparisons of this kind we find that throughout the animal kingdom, with very few exceptions, wherever the sexes are separate and differ from each other, the males of allied species differ from each other more than the females do, and the adult male differs more than the adult female from the young. This law is so pronounced and conspicuous that its existence has long been recognized by all naturalists.

We also find that organs which are confined to males, or which are of more importance or are more perfectly developed in the males than they are in the females, are very much more likely to give rise to hereditary modifications than parts which are confined to or are most developed in females; that a part which is thus confined to males is much more likely to vary than a similar female part; that males are, as a rule, more variable than females; and that the male leads and the female follows in the evolution of new races.

The scientific accuracy of most of these generalizations regarding secondary sexual characters has long been

recognized, although no one, so far as I know, has attempted to trace them back to a fundamental law of heredity. On the contrary, most of the authors who have discussed them have treated them rather as special cases than as the results of a general principle, and analysis shows that none of the explanations which have been advanced are sufficiently broad to cover the whole ground.

Daines Barrington and Wallace have held that the explanation of the fact that male birds and male insects are often so much more brilliantly colored and conspicuously ornamented than the females is to be found in the fact that the female, while laying her eggs or while incubating, is much more exposed to the attacks of enemies than the male, and that inasmuch as the perpetuation of the race depends upon the safety of the females at this time, natural selection has gradually exterminated the conspicuous females, and has preserved those with the least striking colors.

We know, however, that the male is usually more brilliantly colored than the female among reptiles which do not incubate, and even among certain fishes where the male attends to the eggs and young. It is therefore clear that Wallace's explanation stops short of the whole truth, and Darwin's exhaustive review of the subject seems to prove that among birds it is the male and not the female which has been directly modified.

Darwin believes that the greater modification of the males as compared with the females is due to sexual selection. The males have struggled with each other for the possession of the females, or have been selected by the females, and this process long continued is believed by him to have resulted in the perpetuation of the strongest, best armed, or most attractive males.

It is plain that sexual selection must have the effect which Darwin attributes to it, but the fact that even in choice breeds of domesticated animals which are mated according to the wishes of the breeder, and not according to their own selection, the males are more modified than the females, shows that behind the action of sexual selection some more profound law must exist.

Darwin believes that this explanation is to be found in the fact that the male usually has stronger passions than the female, and is consequently more exposed to the action of natural selection. He says that the perpetuation of the race depends upon the existence of the sexual passion, and that, since the male must in most cases seek the female, the most eager males have left the greatest number of offspring, and have thus become selected.

When we bear in mind the fact that the parental instinct is fully as important to the race as the sexual instinct, and that this is usually most developed in the female, we see that the failure of the female to undergo modification for the good of the species as frequently as the male cannot be explained without the recognition of some more general law. The singular history of secondary sexual characters receives a ready explanation by the law of heredity, for this law leads us to look to the cells of the male body for the origin of most of the variations through which the species has attained to its present organization.

Since gemmules which originate in a male body are more likely to be transmitted than those formed in a female body, and since gemmules are most likely to be formed in the sex in which an organ is of most functional importance, and therefore most subject to disturbing influences, we can readily see why a part which is im-

portant to males should vary more than a part which is important to females.

We are thus able to understand the great difference in the males of allied species, the difference between the adult male and the female or young, and the great diversity and variability of secondary male characters, and we should expect to find, what actually is the case, that among the higher animals, when the sexes have long been separated, the males are more variable than the females.

In the chapter on the intellectual differences between men and women, I have shown that those philosophical writers who have devoted especial attention to the subject have reached conclusions which are exactly what our hypothesis would lead us to expect. The view that the male mind is the progressive element in intellectual development, and the female mind the conservative element, accords with the views which have been generally recognized and accepted by the common consent of mankind, and although our opinions upon this very complicated subject may possibly be very far from accurate, a certain conformation to the demands of our hypothesis cannot be denied.

The facts relating to hybrids, to variation, to the secondary sexual characters of animals, and to the intellectual differences between men and women, which are stated at some length in chapters V. to IX., cover a very wide and diversified field, and any law which groups and explains them all is certainly worthy of careful examination. The most candid review which I am able to give to the evidence from all these sources, convinces me that the explanation which I have offered in this book is at least a step in the right direction, and that whether it be accepted in its present form or not, it does serve to en-

large our insight into the hidden relations between the phenomena of nature.

Chapter XI. is devoted to an examination of the law of natural selection, as modified by the law of heredity, and I have here attempted to show that the acceptance of this secondary law will remove the most serious objections to the view that our present forms of life have been brought into existence through the survival of the fittest variations, and I have also called attention to the fact that the law of heredity is itself a result of the law of natural selection.

No one can deny that there are grave objections to the law of natural selection in its original form. Darwin admits this in many places, and able but dissenting critics have stated most of these objections with great ability. The evidence for the law of natural selection is so many sided, so extensive, and so satisfactory, that we may fairly conclude that the difficulties will disappear with greater knowledge, and as none of its hostile critics have proposed anything whatever to take its place, the difficulties which they have pointed out have hardly received from naturalists the attention which they deserve.

One of the most serious objections is that natural selection cannot effect any permanent modification of a race, unless great numbers of individuals vary in essentially the same way at nearly the same time, and that the chances against this are great beyond computation if variations are purely fortuitous in Darwin's sense of the word.

Darwin has acknowledged the weight of this objection, and there is no escape from the conclusion that natural selection fails to account for the origin of species, unless we can show that many individuals tend to vary at the same time. According to our view, the production of

gemmules and the consequent variations are due to the direct action of changed conditions upon certain cells of the body, and any change which affects all the individuals of a species will cause the same part to vary in all of them at the same time. This objection to the law of natural selection is thus entirely removed.

The evolution of a complicated organism, or the modification of any part which includes a number of complicated structures, without destroying their harmonious adjustment to each other, demands a very great number of variations, and if these are fortuitous, we may well doubt whether there has been time enough for the evolution of life by natural selection. According to our theory of heredity, a change in one part of the body is in itself a cause of variation in related parts; and as changes thus tend to occur where and when they are needed, the time which is demanded for the evolution of a complicated organ by natural selection is brought within reasonable limits, and one of the most fundamental objections is thus completely removed.

There are many reasons for believing that variations under nature may not be so minute as Darwin supposes, but that evolution may take place by jumps or saltations. According to our view a change in one part will disturb the harmony of related parts, and will cause their cells to throw off gemmules. A slight change in one generation may thus become in following generations a very considerable modification, and there is no reason why natural selection should not be occasionally presented with great and important saltations.

The law of heredity also enables us to understand the occasional occurrence of parallel or analogous variation, and the parallel evolution of polyphyletic-groups.

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